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STRASBURGER'S

TEXT-BOOK OF BOTANY

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SIXTH ENGLISH EDITION

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PREFATORY NOTE

THE original authors of this text-book as it appeared in 1894 were Professors Eduard Strasburger, Fritz Noll, Heinrich Schenck, and A. F. W. Schimper. The death of Professor Strasburger renders it inaccurate to give his name as an author of the work. His position as the original founder of the text-book requires to be recorded, and is therefore indicated by the name Strasburger's Text-Book, which has been in current use in this country. In the present edition the division on Morphology is by Professor Fitting, that on Physiology by Professor Sierp, that on Thallophyta, Bryophyta, and Pteridophyta by Professor Harder, and that on Spermatophyta by Professor Karsten. Their names are therefore given as the authors on the title-page.

The first edition of the English translation was the work of Dr. H. C. Porter, Assistant Instructor of Botany, University of Pennsylvania. The proofs of this edition were revised by Professor Seward, M.A., F.R.S. The second English edition was based upon Dr. Porter's translation, which was revised with the fifth German edition. The third English edition was revised with the eighth German edition, the fourth English edition with the tenth German edition, and the fifth English edition with the fourteenth German edition. The present edition has been similarly revised throughout with the seventeenth German edition. Such extensive changes, involving the rewriting of all four sections, have, however, been made in the work since it was first translated that it seems advisable to give in outline the history of the English translation instead of retaining Dr. Porter's name on the title-page.

The official plants mentioned under the Natural Orders are those of the British Pharmacopoeia instead of those official in Germany, Switzerland, and Austria, which are given in the original. I am indebted to my colleague Mr. W. O. Howarth for assistance in making this alteration.

My colleague Mr. L. J. F. Brimble has kindly read the proofs of the section on Physiology, and I have to thank him for a number of helpful suggestions.

WILLIAM H. LANG.

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INTRODUCTION

ORGANISMS are distinguished as animals and plants, and a corresponding division of Biology is made into the sciences of Zoology and Botany.

The green, attached, flowering, and fruiting organisms are distinguished as plants in contrast to animals, which are usually capable of free movements and seek and devour their food. Easy as it appears on a superficial acquaintance to draw the boundary between plants and animals, it is really very difficult. In the case of those very simply constructed organisms with little external or internal differentiation, which are usually regarded as lowest in the scale, it is often impossible to decide in which kingdom they should be classed. The following important properties are in fact common to both animals and plants:

1. They are both composed of MICROSCOPICALLY SMALL CHAMBERS or CELLS.

2. They AGREE IN THEIR MOST IMPORTANT VITAL PROCESSES, in nutrition and growth, development and reproduction. A plant also respires with the production of heat, and exhibits powers of movement and irritability of various kinds.

3. This profound agreement in the manifestations of life in plants and animals becomes less surprising when it is realised that THE LIFE OF BOTH IS ASSOCIATED WITH A VERY SIMILAR UNDERLYING SUBSTANCE, THE PROTOPLASM OF THE CELLS.

These and many other facts indicate that plants and animals are really related. This assumption of a GENETIC RELATIONSHIP finds its expression in the THEORY OF DESCENT, which is a fundamental biological theory. The idea of a gradual evolution of more complicated living beings from those of simpler construction was familiar to the Greek philosophers; and was advocated in the beginning of the nineteenth century by the French zoologist, LAMARCK. It was especially through the work of CHARLES DARWIN ([1]), who accumulated evidence for a reconsideration of the whole problem of organic evolution, that the belief in the immutability of species was finally destroyed. From the study of the fossil remains of animals and plants it has been established that in earlier geological periods forms of life differing from those of the present age existed on the earth. This leads to the conclusion that all living animals and plants have been derived by modification from previously existing forms. This leads to the further conclusion that organisms are more or less closely RELATED to one another, and that the union of species in a genus, of genera into families, and of families into higher groups in a "natural" system, serves to give expression to the degrees of relationship existing between them. The evolutionary developments, *i.e.* the transformations which an organism has undergone in its past generations, are termed its PHYLOGENY. The development passed through by the individual in attaining the adult condition is distinguished as its ONTOGENY. It is assumed on the theory of descent that the more highly organised plants and animals had their ultimate, common, phylogenetic origin in forms which perhaps resembled the simplest still existing. The phylogenetic development proceeded from these, on the one hand in the direction of the higher animals, and on the other in the direction of well-defined plants. On this assumption, which is supported by the properties which animals and plants have in common and by the impossibility of drawing a sharp line between animal and plant in the lowest groups, all living beings form one NATURAL KINGDOM.

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[1] The small figures in brackets refer to the Index of Literature at the end of the volume, which will be of value to those wishing to pursue the subject further.

As distinctly marked characteristics of plants which have arisen in the course of their phylogeny, the external development of the surface of the body, which serves to absorb the food in plants (as contrasted with the internal body surface to which the mouth gives entrance in animals), the cellulose walls of vegetable cells and the green chromatophores of plant-cells may be mentioned. By means of the green colouring matter, plants have the power of producing the organic materials of their bodies from inorganic compounds, and are thus able to exist independently; while animals are dependent, directly or indirectly, for their nourishment, and so for their very existence, on plants. Another characteristic of plants is the unlimited duration of their ontogenetic development, which is continuous at the growing points during their whole life. That none of these criteria are alone sufficient for distinguishing plants from animals is evident from the fact that all the Fungi are devoid of green pigment, and, like animals, are dependent on organic food-material. They are, however, placed in the vegetable kingdom, since they can be phylogenetically derived from green plants.

It is, however, impossible to give any definition of "plant" and "animal" that shall hold strictly in all cases. In this connection it is necessary to be satisfied with the knowledge that among the more familiar living beings the Bacteria, Algae, Fungi, Lichens, Mosses, Ferns and Seed-plants are placed in the VEGETABLE KINGDOM, and are thus the subject matter of Botany.

A distinction between organisms and non-living bodies is much more easy. We know no living being in which protoplasm is wanting, while active protoplasm is not to be demonstrated in any lifeless body. Since in the sphere of organic chemistry sugars have been synthesised and the way towards the synthesis of proteids opened up, there is increased justification for the assumption that protoplasm also had an inorganic origin, for the elements it contains all occur in inorganic nature. In ancient times such a "spontaneous generation" was regarded as a possibility even for highly organised animals and plants. It was a widely-spread opinion, shared in by ARISTOTLE himself, that such living beings could originate from mud and sand. It is now known from repeated experiments that even the most minute and simplest organisms with which we are acquainted do not arise in this way but only proceed from their like. Living substance may, however, have arisen from non-living at some stage in the development of the earth, or of another planet, when the special conditions required for its formation occurred. The difficulties associated with this idea of a spontaneous generation remain. In order that the organic world should have proceeded from this first living substance, the latter must from the beginning have been able to nourish itself and to grow. It must also have been capable of reproduction, *i.e.* of multiplying by separation into a number of parts, and further of acquiring new and inheritable properties. In short, this original living substance must have already possessed all the characteristics of life.

Botany may be divided into a number of parts. MORPHOLOGY is concerned with the recognition and understanding of the external form and internal structure of plants. PHYSIOLOGY investigates the vital phenomena of plants. Both morphology and physiology take into consideration the relation of plants to the environment and the external conditions, and endeavour to ascertain whether and how far the structure and the special physiology of each plant can be regarded as adaptations to the peculiarities of its environment. These parts of morphology and physiology are often separated from the rest under the name ECOLOGY. SYSTEMATIC BOTANY deals with the description of the kinds of plants and with the classification of the vegetable kingdom. The GEOGRAPHY OF PLANTS has as its objects to determine the distribution of plants on the surface of the earth and to elucidate the causes of this. Extinct plants form the subject matter of PALAEOPHYTOLOGY. All these are subdivisions of PURE OF THEORETICAL BOTANY.

Botany is also concerned with rendering the knowledge so obtained useful to mankind. There have thus to be added to the divisions of pure botany the numerous branches of APPLIED BOTANY, *e.g.* the study of medicinal plants and drugs, of vegetable food-substances, of technically valuable plants and their products, agricultural botany, and that part of plant-pathology which is concerned with the prevention and treatment of diseases of plants.

In this work, which is primarily concerned with pure botany, a division is made into a general and a special part. The object of GENERAL BOTANY is to ascertain the most distinctive properties of plants in general or of the main groups. General botany is further divided into the two sections treating of morphology and physiology.

The object of SPECIAL BOTANY is to describe the structural features, the methods of reproduction, and the modes of life of the various groups of plants. It attempts also to express the more or less close relationships which exist between plants both living and extinct by arranging them in as "natural" a system as possible. In this special part a few main facts as to some branches of applied botany, especially regarding pharmaceutical plants, are inserted. Lastly, facts regarding the geography of plants are included, though no connected account of it is given.

PART I

GENERAL BOTANY

DIVISION I

MORPHOLOGY

GENERAL BOTANY

DIVISION I

MORPHOLOGY

MORPHOLOGY is the study of the external form and the internal structure of plants and the ontogenetic development of the plant body as a whole and of its members. In seeking to establish the significance and the phylogenetic origin of the parts of plants and the causes of the formative processes, it aims at a scientific understanding of the forms of plants.

1. The outer and inner construction of a living being can only be understood when it is clearly realised that the animal or plant is a living ORGANISM, *i.e.* a structure the main parts of which are not meaningless appendages or members, but necessary ORGANS by the harmonious co-operation of which the life of the whole is carried on (2). Almost all the external parts of plants, and of animals also, are such organs performing definite functions. They can, however, only play their parts in the service of the whole organism when they are appropriately constructed, or, in other words, when their structure corresponds with, or is adapted to, their functions. Since the various parts of the higher plants have diverse functions, it is easy to see why the plant is composed of members very unlike in form and structure.

In order to fully understand the construction of an organism it is further necessary to know the conditions under which it lives and to be acquainted with its environment. Every plant, or animal, has structural peculiarities which enable it to live only under certain conditions of life which are not provided everywhere on the earth's surface. The conditions of life, for example, are very different in water from those in a desert, and water-plants and desert-plants are very differently constructed. They can only succeed under their usual conditions or such as are similar, and the desert-plants would not grow in water or the water-plants under desert conditions. The life of an organism is thus only possible when its construction is in agreement with its environment, and it is ADAPTED TO THE CONDITIONS OF LIFE.

More penetrating morphological investigation soon shows that, while almost every member of the plant body has its functions, every peculiarity in construction cannot be regarded as adapted to these functions or to the environment. This can only be said of some of the characters of any part of the plant; for example, the abundance of the green pigment and the expanded form of foliage leaves stand in relation to the main functions of the leaf. Such characters are spoken of as useful to the organism or as adaptive. Many other characters are indifferent, such as, for example, the nature of the margin of leaves, described as entire, serrate, crenate, etc. Others may even be unfavourable so long as they are compatible with life, *e.g.* the absence of the green pigment from large portions of the leaf in many cultivated forms of Sycamore. A character may be useful in one species while it is indifferent or even harmful in another. These facts show clearly what care is requisite in judging of the significance of organic forms and structures; it is no easy matter to prove such assumptions by investigation (³)

2. There is a second direction in which morphology endeavours to attain a scientific understanding of the forms of plants. All existing plants are regarded as genetically related, the most highly organised with their diverse organs having gradually arisen phylogenetically from simple, unsegmented forms. The organism and its parts have thus undergone manifold transformations in which, for example, particular organs by change of their structure took over new functions or became adapted to new conditions of life. It is thus a very important object of morphology to derive phylogenetically one form from another. Since the genetic development cannot be directly traced but has to be inferred, morphology is dependent on indirect methods in this problem. The most important indications are obtained by the study of the ontogeny of organisms and by the comparison of existing plants with one another and with those that lived in preceding ages. Within certain limits the ontogeny often repeats the phylogeny and thus contributes to the discovery of the latter. Comparative study connects divergent forms by means of intermediates. Since, however, the ontogeny never repeats the phylogeny completely or without alterations, and the connecting forms are often wanting, the results of morphology in this direction are correspondingly imperfect.

When the conviction has been reached after full investigation that diversely formed members of the plant-body had a common phylogenetic origin, the hypothetical form from which we derive them is termed the PRIMITIVE FORM, and the changes undergone by it in the course of descent its METAMORPHOSES. One of the most important results of morphology is the demonstration THAT THE VARIOUSLY FORMED PARTS OF EVEN THE MOST HIGHLY DIFFERENTIATED PLANTS ARE TO BE TRACED BACK TO A FEW PRIMITIVE FORMS, for example, the external parts of the more highly organised plants to root, stem, and foliage leaf, and the internal parts of all plants to cells. Those organs which have developed phylogenetically from a common primitive form are spoken of as HOMOLOGOUS, however different they may appear. The same morphological value is ascribed to them. For example, foliage leaves and the leaves of the flower (sepals, petals, stamens, and carpels) are homologous, and this extends to the leaf-tendrils (Fig. 202) and the leaf-thorns (Fig. 190). Organs of completely different structure and functions can thus be homologous. On the other hand, organs with similar construction and functions (*e.g.* tubers (Figs. 196, 198, 199), thorns (Figs. 190, 192, 193), tendrils (Figs. 201-203)) have often been genetically derived from different primitive forms. Such organs are spoken of as ANALOGOUS (for examples cf. p. 55 ff.). Little differentiated structures with ill-defined functions, which have retrograded from more perfect ones, are termed REDUCED organs.

3. Lastly, it is an aim of morphology to ascertain the causes or conditions which underlie the ontogeny and phylogeny of plants. In this way it may be possible to ascertain clearly how in the course of descent adaptive characters have arisen. The study which concerns itself with such questions is EXPERIMENTAL MORPHOLOGY. Most of the problems of this are more conveniently dealt with as a section of physiology in relation to the other vital processes of the plant (developmental physiology).

Morphology may be divided into external morphology and internal morphology or anatomy. Since it is desirable to regard the parts of the plant as organs with definite functions, it is necessary to show the intimate connection that frequently exists between the function of an organ and both its form and internal structure. From the outset we must be concerned with the plant as a living organism and not as a dead structure. The protoplasm as the substance manifesting the phenomena of life is, as a rule, enclosed in the cells which can be regarded as the elementary parts of the organism. The part of morphology which is concerned with the structure of cells is termed CYTOLOGY and will be dealt with first. The tissues formed by associated cells will then form the subject of a second part of morphology to which the name HISTOLOGY is given. Lastly, ORGANOGRAPHY deals with the external members of the plant regarded as its organs, taking into consideration both their external form and internal structure.

SECTION I

CYTOLOGY

I. FORM AND SIZE OF CELLS

The cells of plants are usually microscopically small chambers, of spherical, cubical, polyhedral, or prismatic shape; elongated fibres and tubes are also of frequent occurrence. Their mean diameter is between the hundredth and the tenth of a millimetre. Owing to their small size it was long before the existence of cells was recognised. Occasionally cells attain a much greater size. Thus some spindle-shaped cells (sclerenchyma fibres), adapted to special functions, are 20 cm. long, while laticiferous tubes may be some metres in length. In contrast to the cells of the animal body those of the plant have usually a cell-wall or cell-membrane enclosing the cell-cavity or lumen. The most important part of the cell is the protoplast or cell-body, since this is the living portion of the cell. On this account it is now natural to think rather of the living protoplast than of its enclosing chamber as the cell; a cell-wall is completely wanting in the case of many "naked cells." In dead cells, the protoplasts have almost or completely disappeared, and such cells contain only water or air. These dead cells are however essential in the construction of the more highly organised plants, in which they form the water-conducting tracts and contribute to mechanical rigidity.

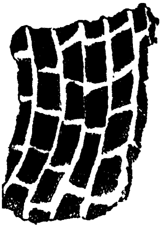

FIG. 1.—Copy of a part of HOOKE'S illustration of bottle-cork, which he described as "Schematism or texture of cork." Cf. Fig. 55.

It was due to the investigation of the cell-walls that cells were recognised first in plants. An English micrographer, ROBERT HOOKE, was the first to notice vegetable cells. He gave them this name in his *Micrographia* in the year 1667, because of their resemblance to the cells of a honeycomb, and published an illustration of a piece of bottle-cork having the appearance shown in the adjoining figure (Fig. 1). The Italian, MARCELLO MALPIGHI, and the Englishman, NEHEMIAH GREW, whose works appeared almost simultaneously a few years after HOOKE'S *Micrographia*, were the true founders of vegetable histology. The living contents of the cell, the protoplast, was not recognised in its full significance until the middle of last century. Only then was attention turned more earnestly to the study of cytology, which was especially advanced by SCHLEIDEN, HUGO v. MOHL, NÄGELI, FERDINAND COHN, MAX SCHULTZE, and STRASBURGER.

II. THE LIVING CELL-CONTENTS. THE PROTOPLAST (4)

A. The Constituent Parts of the Protoplast

If a thin longitudinal section of the growing point of the stem of one of the higher plants is examined under the high power of the microscope it is seen to consist of nearly rectangular cells (Fig. 2), which are full of protoplasm and separated from one another by delicate walls These cells have the shape of small cubes or prisms.

In each of the cells a spherical or oval body, which fills a large part of the cell-cavity, is distinguishable. This body (*k*) is the NUCLEUS of the cell. The finely granular substance (*pl*) filling in the space between the nucleus (*k*) and the cell-wall (*m*) is the cell-plasm, or CYTOPLASM. In the cytoplasm there are to be found around the nucleus a number of colourless and highly refractive bodies: these are the PLASTIDS or CHROMATOPHORES (*ch*). THE NUCLEUS, CYTOPLASM, AND CHROMATOPHORES ARE THE LIVING CONSTITUENTS OF THE CELL. They form together the protoplasm of the living cell-body or PROTOPLAST. The nucleus and the chromatophores, which are always embedded in the cytoplasm, may be regarded as organs of the protoplast, since they perform special functions. In the lowest plants (Cyanophyceae and Bacteria) a true nucleus is not present (5). Chromatophores are wanting in the Bacteria and Fungi as in all animal cells.

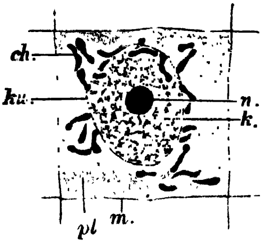

FIG. 2.—Embryonic cell from the root-tip of the Oat. *k*, Nucleus; *kw*, nuclear membrane; *n*, nucleolus; *pl*, cytoplasm; *ch*, chromatophores; *m*, cell-wall. (Somewhat diagrammatic. × about 1500. After LEWITZKY.)

In many animal cells an additional constituent of the protoplast has been demonstrated as a small body, which is called a CENTRIOLE, in the immediate neighbourhood of the nucleus. Similar bodies are found in the vegetable kingdom in the cells of some Cryptogams, but are not of general occurrence even in them.

It is only the embryonic cells of the plant, as they are met with in the apices of stem and root, which are thus completely filled with protoplasm. This does not hold for the fully developed cells of the plant which arise from these by growth in size and alterations of shape. During this transformation to cells of the permanent tissues the embryonic cells of plants, unlike those of animals, become poorer in protoplasm, since this does not increase in proportion to the growth of the cell. In every longitudinal section of the growing point of the stem it can be seen that at some distance from the tip the enlarged cells have already begun to show cavities or VACUOLES (*v* in *A*, Fig. 3) in their cytoplasm. These are filled with a watery fluid, the CELL-SAP. The cells continue to increase in size, and usually soon attain a condition in which the whole central portion is filled by a single large sap-cavity (*v* in *B*, Fig. 3). The cytoplasm then forms only a thin layer lining the cell-wall, while the nucleus occupies a parietal position in the peripheral cytoplasmic layer (Fig. 3 *B*, *k*). At other times, however, the sap-cavity of a fully-developed cell may be traversed by bands and threads of cytoplasm; and in that case the nucleus is suspended in the centre of the cell (Figs. 5, 10). But whatever position the nucleus may occupy, it is always embedded in cytoplasm; and there is always a continuous peripheral layer of cytoplasm lining the cell-wall. This cytoplasmic peripheral layer is in contact with the cell-wall at all points, and, so long as the cell remains living, it continues in that condition. In old cells, however, it frequently becomes so thin as to escape direct observation (Fig. 10), and is not perceptible until some reagent, such as concentrated solutions of salt or sugar, which attracts water and causes it to recede from the wall, has been employed (plasmolysis, cf. p. 219).

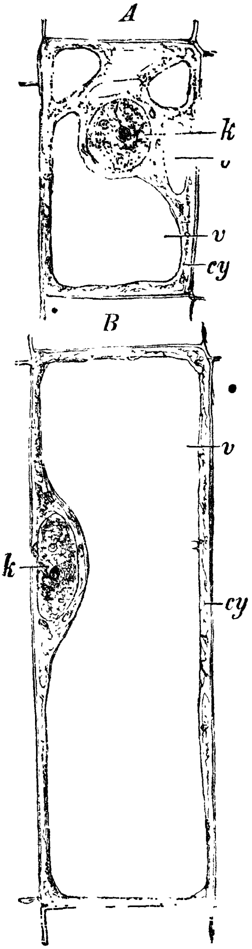

FIG. 3.—Two cells taken at different distances from the growing point of a phanerogamic shoot. *k*, Nucleus; *cy*, cytoplasm; *v*, vacuoles, represented in *B* by the sap cavity. (Somewhat diagrammatic. × circa 500. After STRASBURGER.)

B. Physical Properties of the Protoplast

In order to facilitate an insight into the physical properties and especially the conditions of aggregation of protoplasm, attention will first be directed to the SLIME FUNGI (Myxomycetes), a group of organisms which stand on the border between the animal and vegetable kingdoms. The Myxomycetes are characterised at one stage of their development by the formation of a PLASMODIUM, a large, naked mass of protoplasm (Fig. 4). This consists of reticulately connected strands composed of a clear ground-substance, within which are numerous granules; it has the consistence of a tenacious fluid. The protoplasm within the firmer and denser boundary layer of the strands exhibits an active streaming movement. The plasmodium can protrude and withdraw processes of its margin and thus creep about. When it encounters a foreign body it can include and when possible digest it, expelling the indigestible remains. All these phenomena of movement are elementary vital processes and it is not yet known in what way they come about.

Similar streaming movements of the protoplasm can often be recognised in the living cells of the higher plants (6). In these also the protoplasm is a more or less tenacious fluid and if freed from the cell-wall takes the form of a spherical drop. A distinction is made between CIRCULATION and ROTATION of the protoplasm in such cells. In those in which rotation occurs, *e.g.* the cells of many water-plants, the protoplasm forms a layer lining the cell-wall, and the single continuous current moves in a constant direction within the wall. Circulation on the other hand is found in the cells of land-plants the vacuole of which is traversed by lamellae or strands of protoplasm. The streaming movement, which may be in various directions that can be reversed, occurs in the strands and also in the layer lining the wall.

When the protoplasm is in rotation, the cell-nucleus and chromatophores are usually carried along by the current, but the chromatophores may remain in the boundary layer, which does not undergo movement. This is the case with the Stoneworts (Characeae), the long internodal cells of which, especially in the genus *Nitella*, afford good examples of well-marked rotation. A particularly favourable object for the study of protoplasm in circulation is afforded by the staminal hairs of *Tradescantia virginica* (Fig. 5). The cytoplasmic threads which traverse the sap-cavity gradually change their form and structure, and may thus alter the position of the cell-nucleus.

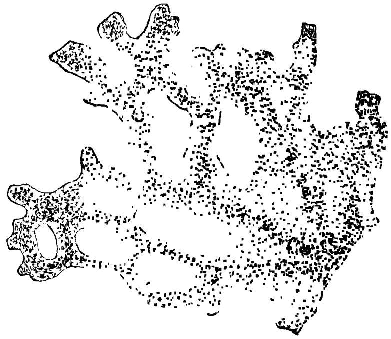

FIG. 4.—Portion of a full-grown plasmodium of *Chondrioderma difforme*. (× 90. After STRASBURGER.)

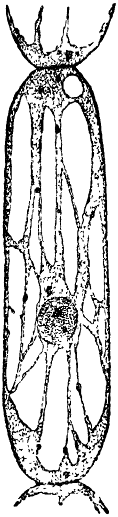

FIG. 5.—Cell from a staminal hair of *Tradescantia virginica*, showing the nucleus suspended by protoplasmic strands. (× 240. After STRASBURGER.)

The movements often commence or become more active when the protoplasm is stimulated, by illumination, by the presence of chemical substances, or by the wounding involved in the preparation of sections.

Movements in limited regions of protoplasts are seen in many of the lower Algae, especially in their swarm-spores. Near the anterior end of the swarm-spore the protoplasm may contain one or several minute pulsating vacuoles which appear and disappear rhythmically at short intervals. They empty suddenly, then reappear and slowly increase to their full size (Fig. 330, 1 *v*). The protoplast of the swarm-spore also possesses one or a number of threadlike contractile processes (cilia, flagella) which vibrate rapidly and serve as the motile organs of the cell (*cf.* Figs. 308, 310-312, 330).

Only within a narrow range of temperature is the protoplast actively alive, and thus capable of movement, though life is preserved through a slightly more extended range. It dies and coagulates, as a rule, at temperatures slightly above 50° C. Alcohol, acids of suitable concentration, solutions of mercuric chloride and of salts of other heavy metals rapidly coagulate the protoplasm, and such substances are largely employed as fixing reagents in microscopical technique (7).

C. Chemical Properties of the Protoplast (8)

Active protoplasm generally gives an alkaline, under certain conditions a neutral reaction, but never an acid one. It is not a simple substance chemically, but consists of a mixture of a large number of chemical compounds some of which are solid and others dissolved in water. Some of these undergo continual changes, upon which undoubtedly many important manifestations of the life of the protoplast depend. The most important components of the mixture are the albuminous substances (proteins, proteids). The protoplasm thus shows the reactions of albumen, and when incinerated gives off fumes of ammonia. In the nuclei, proteids containing phosphorus (nucleoproteids), which are not dissolved by pepsin, predominate. They are also met with in the cytoplasm. The ash left after incineration shows that mineral substances are present in protoplasm.

Products of the dissociation of proteids are always contained in the protoplasm. Other components are enzymes, carbohydrates and lipoids such as fats and lecithin (cf. p. 249), physosterin (aromatic alchohols with the formula $C_{27}H_{45}OH$) and sometimes alkaloids (nitrogenous bases) or glucosides (ester-like compounds of sugar, usually with aromatic compounds).

By the action of a dilute solution of potash, of chloral hydrate, or of eau de javelle, all parts of the protoplast are dissolved. Iodine stains it a brownish-yellow colour; acid nitrate of mercury (Millon's reagent), rose-red. Such reagents kill the protoplasm, after which their characteristic reactions are manifested. These reactions are given by proteid substances, but are not altogether confined to them.

D. Structure of the Parts of the Protoplast

Great assistance in the investigation of the structure of the protoplast is afforded by the processes of fixing and staining. Certain fixing agents harden and fix the protoplasm almost unaltered, but it is necessary to be on guard against the appearance of a structure in the process of coagulation (9).

The importance of staining depends upon the fact that the various constituents of the protoplast absorb dyes with different intensity and hold them more or less firmly when the preparation is washed. As a general rule only dead protoplasm is readily stained. For staining fixed vegetable protoplasts, solutions of carmine, haematoxylin, safranin, acid fuchsin, gentian violet, orange, methylene blue, etc., are employed.

1. The Cytoplasm.—This when highly magnified is seen to consist of a clear, hyaline, more or less tenacious fluid (HYALOPLASM) in which more or less numerous minute drops or granules (MICROSOMES) are embedded. The latter are evidently various products of the metabolism. The hyaloplasm, which when studied, by means of the ultramicroscope appears almost empty optically, is a watery colloidal solution or sol from the point of view of physical chemistry; sometimes it has the properties of a gel. The insight thus obtained into the nature of protoplasm is of fundamental importance. By means of it many of the properties of protoplasm obtain a physico-chemical explanation (10).

An extremely thin boundary layer of hyaloplasm free from granules is found at the periphery of the protoplast, and a similar layer bounds every vacuole present in the cytoplasm. The peripheral boundary layer and the vacuole walls can be formed anew, but are nevertheless very important parts of the protoplast, since they determine the taking up of substances. They are semipermeable membranes, *i.e.* they allow water to pass, but are impermeable or only slightly permeable to many other substances.

It is uncertain whether living protoplasm has a still finer structure that cannot be detected with the microscope or ultramicroscope. In dividing protoplasts fine filaments may appear which cease to be evident in the resting condition of the cell. When fixed and stained the cytoplasm appears homogeneous or, if imperfectly fixed, a reticulate or honeycomb-like structure with embedded granules is formed as in other coagulated colloidal solutions.

In addition to the structures alluded to above, there have recently been demonstrated in the cytoplasm of both embryonic and permanent cells certain filamentous, spindle-shaped or dumb-bell-shaped structures. These are best seen after special fixation and staining, and agree so closely with the CHONDRIOSOMES (mitochondria) of embryonic animal cells that they have been given the same name (11). Probably they include bodies of various nature such as minute vacuoles filled with albuminous substances containing nucleic acid, young chromatophores, etc. They have been observed in some Mosses in the embryonic cells beside the chromatophores, and also in the Fungi.

2. The Nucleus (12) has as a rule a spherical, oval, or lenticular form, but in long cells may be correspondingly elongated; it is sometimes lobed. In embryonic cells its diameter may amount to two-thirds of the total diameter of the protoplast. In full-grown cells of the permanent tissue, on the other hand, the nucleus is much less conspicuous, since it has not increased in size. Large nuclei are found in most Conifers, in some Monocotyledons, and in the Ranunculaceae and Loranthaceae among the Dicotyledons. Secretory cells are as a rule provided with especially large nuclei. On the other hand, the nuclei of the majority of Fungi (Fig. 6) and of many Siphoneae are very small.

While the cells of the higher plants are almost always uninucleate, in the Thallophytes, on the contrary, multinucleate cells are by no means infrequent. In many Fungi (Fig. 6), and in the Siphoneae among the Algae, they are the rule. The whole plant is then composed either of but one single multinucleate cell, which may be extensively branched and exhibit a complicated external form as in *Caulerpa* (Fig. 343), or it may consist of a large number of multi-nucleate cells, forming together one organism, as is the case for many Fungi and for the fresh-water Alga *Cladophora* (Fig. 7).

The living nucleus has a finely dotted appearance. It usually contains one or several larger, round, highly refractive granules or droplets, the use of which is unknown but which are called NUCLEOLI (Fig. 2 *n*). The nucleus, the consistence of which appears to be that of a tenacious fluid, is surrounded by a NUCLEAR MEMBRANE (Fig. 2 *kw*) by which the surrounding cytoplasm is separated from the NUCLEAR CAVITY.

Some insight into the finer structure of the nucleus is obtained from properly fixed and stained preparations. In these a deeply staining reticulum of CHROMATIN (Fig. 13, 1 *n*), which appears to consist mainly of nucleo-proteids, is evident. In many nuclei the reticulum appears to be formed of a substance called LININ that stains feebly, and the chromatin to be embedded in this as minute granules. The nucleoli are situated in the meshes of the network within the nuclear cavity which is filled with the NUCLEAR SAP. The nucleoli stain deeply, but differently from the chromatin.

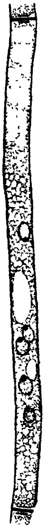

FIG. 6.—Cell of the fungus, *Hypholoma fasciculare*, containing five nuclei. (× 500. After KNIEP.)

In *Spirogyra* and some other Algae, certain Flagellata and Fungi the nucleoli contain a proportion of the chromatin. They are thus not strictly equivalent to the nucleoli of the higher plants, as is further shown by their behaviour in the process of nuclear division ([13]).

It is still unknown what part the nucleus takes in the vital phenomena of the protoplast. It is, however, clear that it is necessary for the maintenance of life in the cell. It also appears to be of great importance as the bearer of the hereditary characters.

3. The Chromatophores ([14]).—In the embryonic cells of the embryo and of growing points, where the chromatophores (Fig. 2 *ch*) are principally located around the nucleus, they first appear as small, colourless, highly refractive bodies of circular, spindle-shaped, or filamentous form. In older cells they attain a further development, as CHLOROPLASTS, LEUCOPLASTS, or CHROMOPLASTS. Since these bodies have the same origin they are all termed CHROMATOPHORES.

(a) Chloroplasts.—In parts of plants which are exposed to the light the chromatophores usually develop into chlorophyll-bodies or chloroplasts. The colour of green plants and their power of assimilating carbon dioxide are due to the chloroplasts. These are generally green granules of a somewhat flattened ellipsoidal shape (Fig. 8 *cl*), and are scattered, in numbers, in the parietal cytoplasm of the cells. All the chloroplasts in the more highly organised plants have this form (chlorophyll grains).

In the lower Algae, however, the chlorophyll-bodies may assume a band-like (Fig. 329 *C*), stellate, or tabular shape; they are often reticulately perforated, *e.g. Cladophora* (Fig. 9). In these cases the chloroplast often includes one or more PYRENOIDS (Fig. 9 *py*); these are spherical protoplasmic bodies, sometimes containing an albuminous crystalloid, and are surrounded by small grains of starch.

After a green plant has been exposed to sunlight for some time its chloroplasts are usually found to contain small starch-grains (assimilation starch, Fig. 15) and frequently oily drops that possibly consist of aldehydes. No structure can be distinguished in the living chlorophyll grains themselves, which have a uniformly green colour.

The green pigment, CHLOROPHYLL, is essential for the decomposition of carbon dioxide in the chloroplasts.

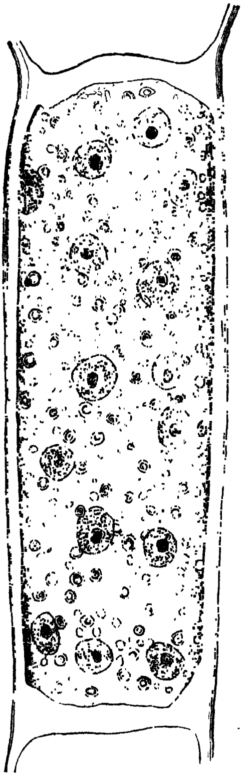

FIG. 7.—A cell of *Cladophora* fixed and stained with carmine. *n*, Nuclei. (× 540. After STRASBURGER.)

Two groups of pigments are always present in the chloroplasts ([15]). There are two closely related green pigments (chlorophyll *a* and *b*) in the proportions of 3 to 1, and a group of yellow pigments. The chlorophylls are esters of phytol, an alcohol of the formula $C_{20}H_{39}OH$, and a tri-carbon acid. They are thus compounds with large molecules containing carbon, oxygen, and hydrogen into the construction of which nitrogen and magnesium enter, but not, as was previously assumed, either phosphorus or iron. The blue-green CHLOROPHYLL *a* has the formula $C_{55}H_{72}O_5N_4Mg$, $+\frac{1}{2}H_2O$, while that of the yellow-green CHLOROPHYLL *b* is $C_{55}H_{70}O_6N_4Mg$. The yellow pigments are the orange-red, crystalline CAROTINS, hydrocarbons of the composition $C_{40}H_{56}$, one of which also occurs in the root of the carrot and the yellow crystalline XANTHOPHYLL (oxide of carotin, $C_{40}H_{56}O_2$).

All these pigments can be extracted from the fresh or dried chloroplasts by various solvents, *e.g.* by acetone or 80-90 % alcohol. A deep-coloured solution containing all the pigments can be most readily obtained by pouring boiling alcohol on fresh leaves. Owing to the contained chlorophyll such a solution is deep green by transmitted light, but blood-red, owing to FLUORESCENCE, by reflected light. Its spectrum (Fig. 242) is characterised by four absorption bands in the less refractive (red) portion and three in the more refractive (blue) half. The individual pigments can be separated by shaking the solution with various solvents. Thus benzol extracts the chlorophyll and accumulates as a green solution above the alcoholic solution which is now yellow. The amount of chlorophyll present in green parts of plants is relatively small, amounting, according to WILLSTÄTTER, to 0·5-1·0 % of the dry substance.

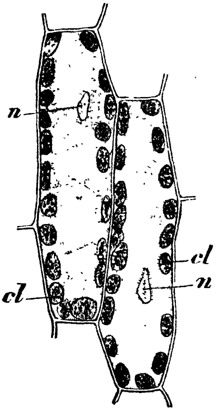

FIG. 8.—Two cells from a leaf of the Moss, *Funaria hygrometrica*. *cl*, Chloroplasts; *n*, nucleus. (× 300. After SCHENCK.)

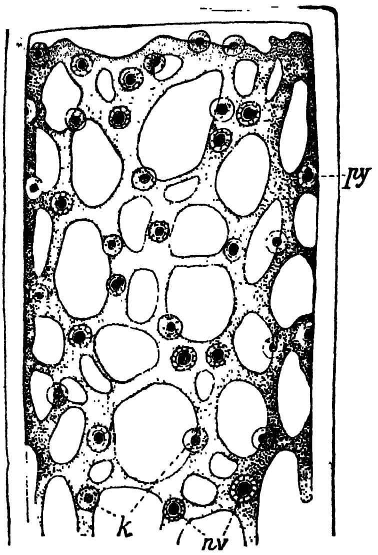

FIG. 9.—Reticulate chloroplast of *Cladophora arcta*. *py*, Pyrenoids; *k*, nuclei. (After SCHMITZ.)

Many Algae (*e.g.* the Blue Green Algae, the Red Algae, and the Brown Algae), are not pure green but have other colours. This is due to various additional pigments in the chloroplasts that more or less obscure the chlorophyll which is however always present.

The variegated forms of some cultivated plants have larger or smaller areas of the leaf of a white or golden colour. The cells here contain colourless or yellow chromatophores instead of the green chloroplasts.

The colourings ([16]) which the leaves of trees assume in autumn before they fall are connected with a breaking down of the chloroplasts and their pigments. The case is different in those Coniferae the leaves of which turn brown in winter and again become green in the spring; the changes undergone by the pigments in the chloroplasts are here reversible. The assumption of a brown colour by dying foliage-leaves is a *post mortem* phenomenon in which brown pigments soluble in water are produced.

In phanerogamic parasites the chloroplasts are replaced by colourless, brownish, or reddish chromatophores, which may, however, in some of these plants still contain a trace of chlorophyll. In the Fungi chromatophores are completely wanting.

(b) Leucoplasts.—In many parts of plants, especially those to which light cannot penetrate, leucoplasts are developed from the rudiments of the chromatophores instead of chloroplasts. They are usually of minute size (Figs. 5, 10 *l*), mostly spherical in shape, but often somewhat elongated in consequence of enclosed albuminous crystals (Fig. 27 *B kr*). If the leucoplasts become exposed to the light, they may change into chloroplasts. This frequently occurs, for example, in the superficial portions of potato tubers. The leucoplasts have the special function of transforming sugar into grains of starch, which appear within them.

(c) Chromoplasts. — These give the yellow and red colour to many parts of plants, especially to flowers and fruits. They arise from the colourless chromatophores of embryonic cells or from previously formed chloroplasts.

Their colour is yellow or orange-red, depending either on xanthophyll or carotin. The pigments are not uniformly dissolved in the chromoplast but form minute droplets (grana) in the colourless plasmatic substance (the stroma). The pigments readily crystallise out and the chromoplasts then become needle-shaped, triangular or rhombic in form (Figs. 11, 12).

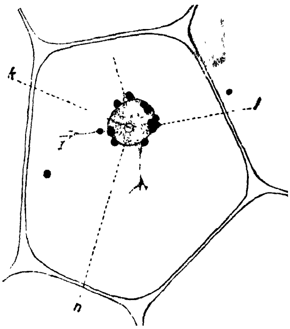

FIG. 10.—Cell from the epidermis of *Rhoeo discolor*. *n*, Nucleus with its nucleolus (*k*), and surrounded by the leucoplasts (*l*). Protoplasmic strands stretch from the nucleus to the layer of protoplasm, which is not represented, lining the wall. (× 240.)

E. Origin of the Elements of the Protoplast (4)

All the living elements of the protoplast, the cytoplasm, the nucleus, and the chromatophores, are never newly formed but always arise from the corresponding elements. They increase in mass by a process of growth, BUT THEY INCREASE IN NUMBER, LIKE THE PROTOPLAST AS A WHOLE, ONLY BY DIVISION OF THEIR KIND. In this way the properties of the living constituents of a germ-cell are transmitted to all the cells of an organism and ultimately to its reproductive cells, the uninterrupted continuity of the life being maintained. The division of the protoplast is usually initiated by the division of the nucleus. In the case of uninucleate cells this intimate association of nuclear- and cell-division is necessary in order to ensure that each daughter cell has a nucleus. In the multinucleate cells (*e.g.* of Algae and Fungi) this is not essential, since each daughter-protoplast would obtain the requisite nuclei, and as a matter of fact cell-division in such cases is often independent of nuclear division.

It sometimes happens that the protoplast of a cell, without dividing, abandons its old cell wall. This process, which is called REJUVENATION of the cell, has nothing to do with cell-division.

The rounding off of the protoplast in a cell of the green alga *Oedogonium*, and its emergence from an opening in the old cell-wall as a naked swarm-spore, is an example of rejuvenation. Another is afforded by the protoplasts of the spores of mosses or ferns and of the pollen-grains of seed-plants surrounding themselves with a new cell-wall within the old membrane, which then perishes.

1. Typical Division of the Protoplast. (a) Nuclear Division.—Except in a few cases, nuclei reproduce themselves by MITOTIC or INDIRECT DIVISION. This process, often referred to as KARYOKINESIS, is somewhat complicated and has been chiefly studied in properly fixed and stained sections.

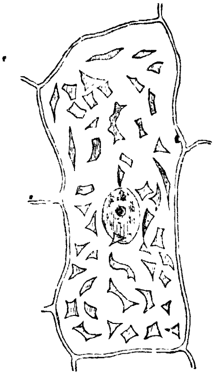

FIG. 11.—Cell from the upper surface of the yellow calyx of *Tropaeolum majus*, showing chromoplasts. (× 540. After STRASBURGER.)

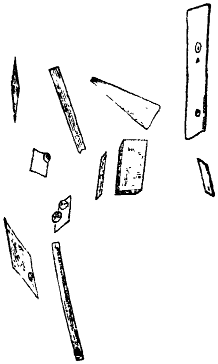

FIG. 12.—Chromoplasts of the Carrot, some with included starch grains. (× 540. After STRASBURGER.)

Indirect Nuclear Division ([12]).—In its principal features the process is similar in the more highly organised plants and in animals. Its stages are represented in a somewhat diagrammatic manner in the following figure (Fig. 13) as they occur in a vegetative cell such as those which compose the growing point.

The fine network of the resting nucleus (Fig. 13, 1 *n*) becomes drawn together at definite points (spireme stage) and separated into a number of bodies (Fig. 13, 2 *ch*), the outline of which is at first irregular. Their form soon becomes filamentous, and the filaments become denser and stain more deeply (3, 4). The filaments are called CHROMOSOMES. Each chromosome undergoes a longitudinal split which continues to become more marked (5). The chromosomes, which become shorter, thicker, and smooth (6), are moved into the plane of division where they constitute the nuclear or equatorial plate (7 *kp*), a stellate figure (aster) which usually lies in the future plane of division of the cell. It is seen in surface view in Fig. 14.

While the nuclear network is separating into the individual chromosomes, cytoplasmic filaments become applied to the nuclear membrane, surrounding it with a fibrous layer. This layer becomes raised up from the nuclear membrane at two opposite points

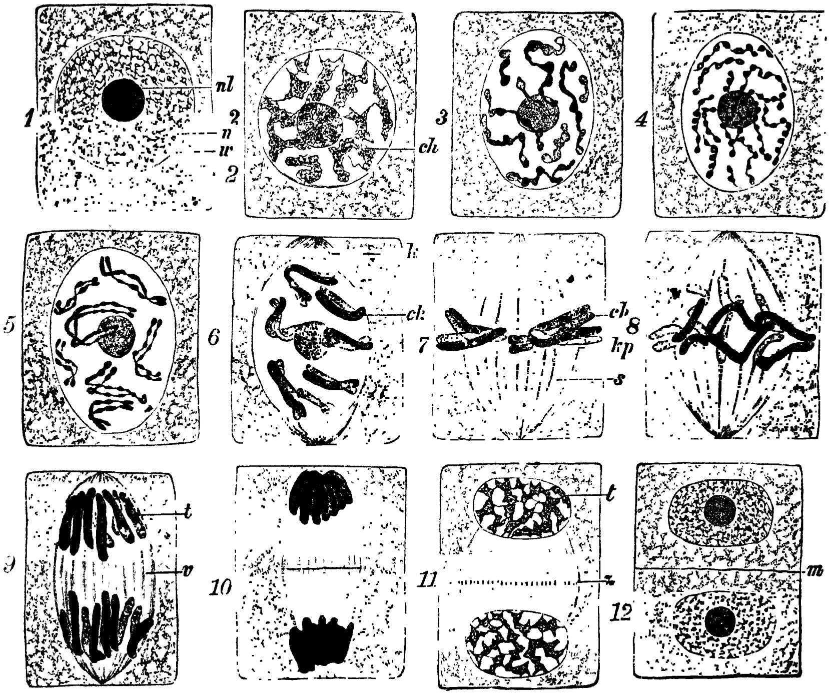

FIG. 13.—Successive stages of nuclear and cell division in a meristematic cell of a higher plant. Somewhat diagrammatic. Based on the root of *Najas marina*, fixed with the chrom-osmium-acetic mixture and stained with iron haematoxylin. *n*, Nucleus; *nl*, nucleolus; *w*, nuclear membrane; *ch*, chromosomes; *k*, polar caps; *s*, spindle; *kp*, nuclear plate; *t*, daughter-nucleus; *v*, connecting fibres; *z*, cell-plate; *m*, new partition wall. The chromatophores are not visible with this fixation and staining. (× about 1000. After CL. MÜLLER.)

(6 *k*) and forms the polar caps. The filaments converge at the poles, where they constitute two pointed bundles. At this stage the nucleoli (*nl*) are dissolved and the nuclear membrane disappears. The fibres proceeding from the polar caps can thus become prolonged into the nuclear cavity (7). Here they either become attached to the chromosomes, or filaments from the two poles may come into contact and extend continuously from the one pole to the other. In this way the nuclear spindle (7 *s*) is formed.

The two halves of each chromosome separated by the longitudinal split now separate in opposite directions (8, 9) as the daughter-chromosomes in order to form the daughter-nuclei (10-12 *t*). During this stage (diaster) the chromosomes are as a rule U-shaped with the bends towards the poles of the spindle. Having reached the poles they crowd together, while the surrounding cytoplasm forms the nuclear membrane delimiting the new nuclei. Within the latter the chromosomes again assume a reticulate structure (di-spireme stage, 11) and unite with one another to form a network (12), within which their individual limits are not distinguishable. We are compelled, however, to assume that the individuality of the chromosomes is not lost. The young nuclei enlarge and one or more nucleoli again appear within them (12).

The end attained by this mechanism of division is that the substance of the nucleus, and especially of the chromosomes, is distributed as equally as possible to the two daughter-nuclei at each division. This is a result of the longitudinal division of each chromosome and the passage of the two halves to the respective daughter-nuclei. From this it may be concluded that the chromatin is especially important for the life of the cell and of the whole organism, and that the chromosomes bear the determinants of hereditary properties, arranged like a string of beads.

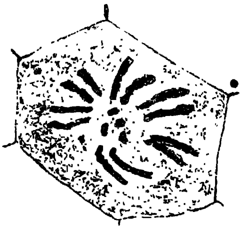

FIG. 14.—Young cell from a transverse section of the root-apex of *Galtonia candicans*, showing a nuclear plate in the polar view. The chromosomes are grouped in pairs. (× 1600. After STRASBURGER.)

The number of chromosomes occurring in any nucleus is a definite one for the particular species of plant. The smallest number of chromosomes which has yet been found in the nuclei of vegetative cells of the more highly organised plants has been six; as a rule the number is much larger (up to 130). The chromosomes of a nucleus frequently differ in size and form (Fig. 14); when such differences exist they persist in successive divisions. These facts indicate clearly that the chromosomes preserve their individuality in the resting nucleus. The variously shaped chromosomes are regarded as bearing different groups of hereditary characters of the kind of plant in question.

The changes occurring in a nucleus preparatory to division are termed the PROPHASES of the karyokinesis. These changes extend to the formation of the nuclear plate. The stage of the nuclear plate, which usually lasts some time, is the METAPHASE. The separation of the daughter-chromosomes is accomplished in the ANAPHASE, and the formation of the daughter-nuclei in the TELOPHASE of the division.

It is uncertain in what way the chromosomes are moved in the process of karyokinesis as described above. STRASBURGER assumed that the fibres of the spindle which appear to end at the chromosomes (traction fibres) by their shortening drew the daughter-chromosomes from the nuclear plate to the poles, while the fibres extending from the one pole to the other were supporting fibres to the spindle. This assumption does not, however, explain the movement of the chromosomes toward the nuclear plate.

In certain reproductive cells of plants and animals the nuclear division proceeds in a special manner and differs from the typical process just described. It is termed the reduction division, or meiosis (cf. p. 189).

Direct Nuclear Division (17).—In addition to the mitotic or indirect nuclear division there is also a DIRECT or AMITOTIC division, sometimes called FRAGMENTATION. Direct division of the nucleus occurs in nuclei which were themselves derived by indirect division. It is essentially a process of constriction, which need not, however, result in new nuclei of equal size. No cell-division follows. Instructive examples of direct nuclear division are afforded by the long internodal cells of the Characeae.

In the case of the Characeae, several successive rapid divisions take place, so that a continuous row of bead-like nuclei often results. Direct nuclear division also occurs in seed-plants, *e.g.* in *Tradescantia*, *Funkia*, *Impatiens balsamina*, etc.

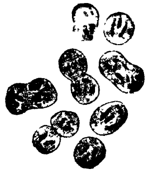

FIG. 15.—Chlorophyll grains from the leaf of the moss *Funaria*, resting, and in process of division. Small included starch grains are present in the grains. (× 540. After STRASBURGER.)

(b) Multiplication of the Chromatophores.—This is accomplished by a direct division, as a result of which, by a process of constriction, a chromatophore becomes divided into nearly equal halves. The stages of this division may best be observed in the chloroplasts (Fig. 15).

(c) Division of the Cytoplasm.—In the uninucleate cells of the higher plants cell-division and nuclear division are, generally, closely associated. The fibres of the spindle extending from pole to pole persist as CONNECTING FIBRES between the developing daughter-nuclei (Fig. 13, 9 *v*), and their number is increased by the interposition of others (Fig. 13, 10, 11). In consequence of this a barrel-shaped figure, the PHRAGMOPLAST is formed. At the same time the connecting fibres become thickened (Fig. 13, 11) at the equatorial plane, and the short rod-shaped thickenings form what is known as the CELL-PLATE. In the case of cells rich in protoplasm or small in diameter the connecting fibres become more and more extended, and touch the cell-wall at all points of the equatorial plane. The elements of the cell-plate unite and form a cytoplasmic limiting layer, which then splits into two. In the plane of separation the new partition wall is formed of cell-wall substance, and thus SIMULTANEOUSLY divides the mother-cell into two daughter-cells (Fig. 13, 12 *m*).

If, however, the mother-cell has a large sap-cavity, the complex of connecting fibres cannot at once become so extended, and the partition wall is then formed SUCCESSIVELY (Fig. 16). In that case, the partition wall first commences to form at the point where the complex of connecting fibres is in contact with the side walls of the mother-cell (Fig. 16 *A*). The cell-plate then detaches itself from the part of the new wall in contact with the wall of the mother-cell, and moves gradually across until the septum is completed (Fig. 16 *B* and *C*); the new wall is thus built up by successive additions from the protoplasm. In elongated cells that divide longitudinally such as those of the cambium the formation of the wall thus proceeds from the middle region where the nucleus is situated (18).

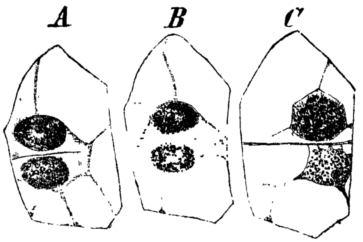

FIG. 16.—Three stages in the division of a living cell of the orchid *Epipactis*. (× 365. After TREUB.)

In the Thallophytes, even in the case of uninucleate cells, the partition wall is not formed within connecting fibres, but arises either simultaneously from a previously formed cytoplasmic plate, or successively, by gradual projection inwards from the wall of the mother-cell. In this form of cell-division the new wall commences as a ring-like projection from the inside of the wall of the mother-cell, and gradually pushing further into the cell finally extends completely across it (Fig. 17). The new wall is formed midway between the daughter-nuclei.

In the naked cells of the Myxomycetes and Flagellates the division results from an active constriction of the protoplast.

2. Deviations from typical Cell Division.

—The main deviations from typical cell-division which are found here and there in the vegetable kingdom are MULTICELLULAR FORMATION, CELL-BUDDING, and FREE CELL FORMATION.

(a) Free Nuclear Division and Multicellular Formation.—The nuclear division in the multinucleate cells of the Thallophytes may serve as an example of free nuclear division, that is, of nuclear division unaccompanied by cell-division. In plants with typical uninucleate cells, examples of free nuclear division also occur. This method of development is especially instructive in the embryo-sac of Phanerogams, a cell, often of remarkable size and rapid growth, in which the future embryo is developed. The nucleus of the embryo-sac divides, the two daughter-nuclei again divide, their successors repeat the process, and so on, until at last thousands of nuclei are often formed. No cell-division accompanies these repeated nuclear divisions, but the nuclei lie scattered throughout the peripheral cytoplasmic lining of the embryo-sac. When the embryo-sac ceases to enlarge, the nuclei surround themselves with connecting strands, which then radiate from them in all directions (Fig. 18). Cell-plates make their appearance in these connecting strands, and from them cell-walls arise. In this manner the peripheral protoplasm of the embryo-sac divides simultaneously into as many cells as there are nuclei. Where

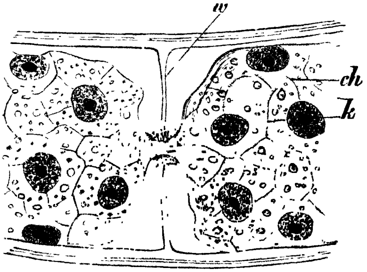

FIG. 17.—Portion of a dividing cell of *Cladophora*. *w*, Newly forming partition wall; *ch*, dividing chromatophore; *k*, nuclei. (× 600. After STRASBURGER.)

the embryo-sac is small and of slow growth, successive cell-division takes place, so that multicellular formation may be regarded as but a shortened process of successive cell-division, induced by an extremely rapid increase in the size of the cell. The reproductive cells of many Algae and Fungi also arise in this way.

(b) Cell-budding.—This is simply a special variety of ordinary cell-division, in which the cell is not divided in the middle, but, instead, pushes out a protuberance which becomes separated from the mother-cell by a wall formed across the constricted region. This mode of cell-multiplication is characteristic of the Yeast plant (Fig. 19); the spores, known as conidia, which are produced by numerous Fungi, have a similar origin (Fig. 410).

(c) Free Cell Formation.—Cells produced by this process differ from those formed by the usual mode of cell-division, in that the free nuclear division is followed by the formation of cells, which have no contact with each other, and in the formation of which the whole of the cytoplasm of the mother-cell is not used up. This process can be seen in the development of the swarm cells of some Algae, in the developing embryo of some Gymnosperms (*e.g.* *Ephedra*), in the formation of the egg-apparatus and antipodal cells in Angiosperms, and also in the formation of the spores of the Ascomycetes. A single nucleus is present to begin with in each ascus of the Ascomycetes. By successive divisions eight nuclei, lying free in the cytoplasm, are derived from this. A definite portion of cytoplasm around each of these nuclei becomes limited from the peripheral protoplasm (periplasm) by a layer, which then forms a cell-wall. Thus eight separate spores arise (cf. Fig. 390). As the researches of Harper (^{19}) have shown, the formation of the peripheral layer proceeds from a centriole-like mass of protoplasm (Fig. 20 *A*) which formed a pole of the spindle in the preceding nuclear division; the nucleus is drawn out towards this. From the centriole-like body radiations proceed (*kp*) which surround the spore as it becomes delimited, and finally fuse to form its peripheral layer (Fig. 20 *B*, *C*, *D*).

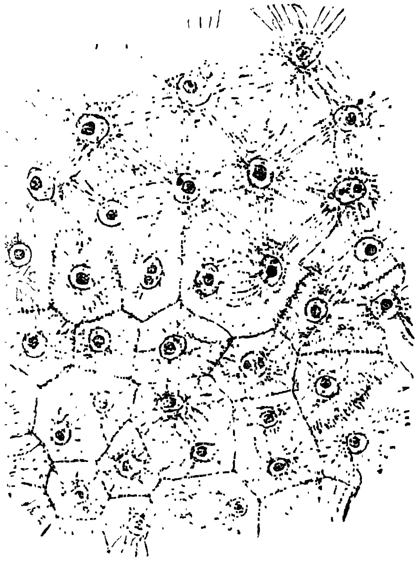

FIG. 18.—Portion of the peripheral protoplasm of the embryo-sac of *Reseda*, showing the commencement of multicellular formation. This progresses from above downwards. From a fixed and stained preparation. (× 240. After STRASBURGER.)

III. THE LARGER NON-LIVING INCLUSIONS OF THE PROTOPLASTS (^{20})

In addition to the minute microsomes which are always present in the cytoplasm, larger non-living inclusions make their appearance in the cytoplasm and chromatophores of all cells as they pass from the meristematic to the mature condition. The cell-sap (Fig. 3 *v*), which in larger or smaller vacuoles is hardly ever absent from a cell of the mature tissues of a plant, has already been mentioned. Besides these droplets of a watery solution, fats and oils and also solid bodies in the amorphous or crystalline condition frequently occur in the cell-sap or the cytoplasm itself. Many of these included substances are of great value in the life of the plant as RESERVE MATERIALS. They are accumulated for future use in considerable quantity in the cells of storage organs (bulbs, tubers, seeds). Others are end products of metabolism which may, however, be of great ecological importance.

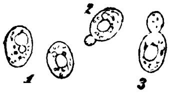

FIG. 19.—*Saccharomyces cerevisiae.* *1*, Cells without buds; *2* and *3*, budding cells. (× 540. After STRASBURGER.)

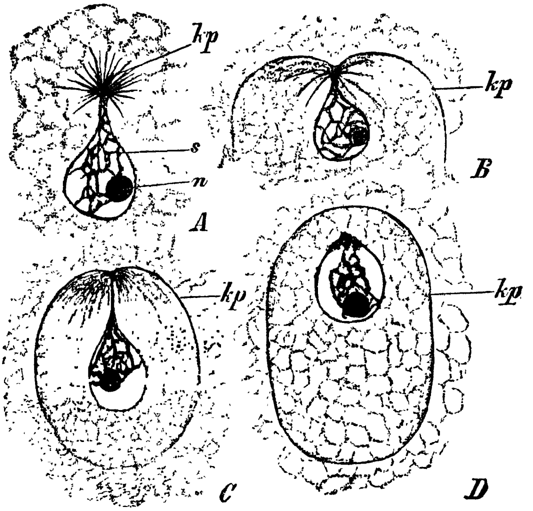

FIG. 20.—Successive stages of the delimitation of a spore in the ascus of *Erysiphe*. *s*, Nuclear network; *n*, nucleolus. (× 1500. After HARPER.)

A. Inclusions of the Cytoplasm

1. Fluid Inclusions of the Cytoplasm. (a) The Cell-Sap.—This name is given to the watery fluid in the larger vacuoles or the single sap-cavity of vegetable cells (Fig. 3). It is more or less rich in various dissolved substances, which may be the same or different from those in the protoplasm. The dissolved substances may differ in the various vacuoles of the same cell.

All cell-sap contains in the first place INORGANIC SALTS, especially nitrates, sulphates, and phosphates. Its reaction is usually acid owing to the presence of ORGANIC ACIDS (*e.g.* malic acid $C_4H_6O_5$, which is constantly present in the leaves of succulent plants, tartaric acid $C_4H_6O_6$, oxalic acid $C_2O_4H_2$, etc), or salts of these.

The SOLUBLE CARBOHYDRATES are especially important constituents of the cell-sap, often as reserve materials. Various SUGARS are the most important. These include di-saccharides ($G_{12}H_{22}O_{11}$) such as cane-sugar and maltose, and monosaccharides ($C_6H_{12}O_6$) such as grape-sugar (glucose). Cane-sugar is frequently stored as a reserve material, as in the sugar-beet, carrot, the stem of the sugar-cane, and other plants from which sugar is obtained. A similar place is taken by the carbohydrate INULIN in the Compositae and by GLYCOGEN in the Fungi.

If preparations containing glucose be placed in a solution of copper sulphate, and, after being washed, are transferred to a solution of caustic potash and heated to boiling, they will give a brick-red precipitate of cuprous oxide. Treated with alcohol, inulin is precipitated in the form of small granules, which may be redissolved in hot water. When portions of plants containing much inulin, such as the root tubers of *Dahlia variabilis*, are placed in alcohol or glycerine, the inulin crystallises out and forms sphaerites (sphere-crystals) which often show distinct concentric stratification.

GLYCOGEN, which is of frequent occurrence in animal tissues, occurs in the Fungi, Myxomycetes, and the Cyanophyceae in the form of droplets. It is a poly-saccharide with the composition $(C_6H_{10}O_5)_n$. It takes the place of other carbohydrates such as starch and sugar. Cytoplasm containing glycogen is coloured reddish-brown with a solution of iodine. This colour almost wholly disappears if the preparation be warmed, but reappears on cooling.

MUCILAGE, which consists of carbohydrates, is often found in the cell-sap of bulbs, as in *Allium cepa* and *Urginea (Scilla) maritima*; in the tubers of Orchids; also in aerial organs (Fig. 21), especially in the stems and leaves of succulents, and also outside the protoplasts in the cell-wall (cf. p. 36).

AMIDES, especially asparagin, occur in the cell-sap as reserve materials or as intermediate products of the metabolism (cf. p. 14).

Highly refractive vacuoles filled with a concentrated solution of TANNIN (21) are of frequent occurrence in the cytoplasm of cortical cells, and may often grow to a considerable size. ALKALOIDS and GLUCOSIDES (cf. p. 14) are also not infrequent in the cell-sap. All these are usually end products of metabolism.

Tannins are mixtures of various aromatic compounds, frequently glucosides; in glucosides in plants gallic acid, gallo-tannic acid (digallic acid or tannin) and ellagic acid are especially widely spread. The dark-blue or green colour reaction obtained on treatment with a solution of ferric chloride or ferric sulphate, and the reddish-brown precipitate formed with an aqueous solution of potassium bichromate, are usually accepted as tests for the recognition of tannins, but are not restricted to them. The tannins are not further utilised in the plant. They often impregnate cell-walls, which then persist and resist decay.

The cell sap is often coloured (22), principally by the so-called ANTHOCYANINS, a group of non-nitrogenous glucosides. They are blue in a weakly alkaline, and red in an acid-reacting cell-sap, and, under certain conditions, also violet (in neutral cell-sap), and even blackish-blue. Alkalies frequently change the colour to green. Anthocyanin can be obtained from the cell-sap of a number of deeply coloured parts of plants in a crystalline or amorphous form.

The anthocyanins are glucosides in which cyanidins (aromatic pigment components, hydroxyl compounds of phenylbenzo-pyrilium, and apparently related to the flavones), are combined with sugar, *e.g.* in the Cornflower cyanidin $(C_{15}H_{10}O_6)$ and in the flower of the Larkspur delphinidin $(C_{15}H_{10}O_7)$. In red flowers the cyanidins are united with acids and in blue flowers with alkalies, while the pigments in violet flowers are neutral.

Less commonly yellow substances, ANTHOCHLORE, are found dissolved in the cell-sap as in the yellow floral leaves of the Primrose and the yellow Foxglove. A brown pigment called ANTHOPHAEINE occurs in the cells of the blackish-brown spots of some flowers. The anthochlores are also glucosides with aromatic pigment components belonging to the flavones, or may be free flavones.

Blood-coloured leaves, such as those of the Copper Beech, owe their characteristic appearance to the united presence of green chlorophyll and anthocyanin.

The different colours of flowers and fruits which often serve to attract animals are due to the varying colour of the cell-sap and also to the different combinations of dissolved colouring matter with the yellow, orange, or red chromoplasts and the green chloroplasts.

(b) Vacuoles containing Fats (Fatty Oils).—These substances are of common occurrence as reserve materials; about nine-tenths of all Phanerogams store them in their seeds often in the form of a very fine emulsion which cannot be optically demonstrated. In seeds especially rich in oil this may form 70 per cent of the dry weight. Especially in the germinating seeds, the oil may form highly refractive droplets (fat-vacuoles) in the cytoplasm.

Fats are mixtures of glycerine esters of fatty acids, especially of palmitic acid ($C_{16}H_{32}O_2$), stearic acid ($C_{18}H_{36}O_2$), and oleic acid ($C_{18}H_{34}O_2$). Since fats provide a greater amount of energy than other storage substances, the space available in storage organs is best utilised for them.

(c) Vacuoles with Ethereal Oils and Resins ([23]).—These also occur as highly refractive droplets. They are found in the cells of many petals. Special cells, often with corky walls and filled with resin or ethereal oils, are found in the rhizomes of certain plants, as for instance in those of *Acorus Calamus* and of Ginger (*Zingiber officinale*); also in the bark, as, for example, of Cinnamon trees (*Cinnamomum*); in the leaves, as in the Sweet Bay (*Laurus nobilis*); in the pericarp and seed of the Pepper (*Piper nigrum*); in the pericarp of Anise (*Illicium anisatum*). Ethereal oils and resins have antiseptic properties. In flowers their scent assists in attracting insects. Under some conditions the oil assumes the crystalline form, *e.g.* in rose petals. Ethereal oils are mixtures of terpenes $(C_{10}H_{16})_{1-n}$ and terpene derivatives with certain esters, phenols, and higher alcohols. Resins and mixtures of terpenes are resin acids which arise from the terpenes by oxidation.

2. Solid Inclusions of the Cytoplasm. (a) Crystals of Calcium Oxalate $Ca(CO_2)_2$.—Few plants are devoid of such crystals ([24]). They are formed in the cytoplasm as end products of metabolism, within vacuoles which afterwards enlarge and sometimes almost fill the whole cell. In such cases the other components of the cell become greatly reduced; the cell-walls at the same time often become corky, and the whole cell becomes merely a repository for the crystal. The crystals may be developed singly in a cell, in which case they are of considerable size (Figs. 125 *k*, 168 *Bk*, 177 *k*), or many minute crystals may fill the cell as a crystalline sand. In other cases they form crystal aggregates (Figs. 125 *k*, 179 *k*), clusters of crystals radiating in all directions from a common centre, or many needle-shaped crystals lie parallel forming a bundle of raphides (Fig. 21). The various types of crystals predominate in different plants.

The SOLITARY CRYSTALS belong to the tetragonal or to the monosymmetric system. The former, with three molecules of water of crystallisation, form as a result of the supersaturation of the solution with calcium oxalate ; the latter (including the raphides) with one molecule of water of crystallisation, result from an excess of oxalic acid.

Crystals of calcium oxalate are soluble in hydrochloric acid, but insoluble in acetic acid.

SILICEOUS BODIES, which are only soluble in hydrofluoric acid, are found in some cells, especially of Grasses, Palms and Orchids.

(b) Aleurone Grains. Proteid Crystals.—Albuminous substances may be stored in a dissolved form in the cell-sap of succulent parts of plants. Thus they can be precipitated by treatment with alcohol in the cells of the potato tuber. In dry structures, such as many seeds, proteid substances occur as solid granules called ALEURONE GRAINS, which are especially large in oily seeds (Fig. 22). They are formed from vacuoles, the contents of which are rich in albumen, and harden into round grains or, sometimes, into irregularly shaped bodies. The albuminous substances of which they consist are mainly globulins (25). A portion of the albumen often crystallises, so that frequently one, and occasionally several, crystals are formed within the aleurone grain. These are especially large in the aleurone grains of the Brazil nut (*Bertholletia excelsa*). In the cereals the aleurone grains, which lie only in the outer cell-layer of the seeds (Fig. 23 *al*), are small, and free from all inclusions. As the outer cells of wheat grains contain only aleurone, and the inner almost exclusively starch, it follows that flour is the richer or poorer in albumen the more or less completely this outer layer has been removed before the wheat is ground. The aleurone layer remains attached to the inner layer of the seed-coat, in the bran.

In aleurone grains containing albumen crystals there may often be found globular bodies termed GLOBOIDS (Fig. 22 *g*), which consist of globulins combined with the calcium and magnesium salt (phytin) of the organic inosithexa phosphoric acid $C_6H_6[O_2P(OH)_2]_6$.

Reactions for aleurone are the same as those already mentioned for the albuminous substance of protoplasm. Treatment of a cross-section of a grain of wheat (Fig. 23) with a solution of iodine would give the aleurone layer a yellow-brown colour.

Albumen crystals usually belong either to the regular or to the hexagonal crystal system. They differ from other crystals in that, like dead albuminous substances, they may be stained, and also in that they are capable of swelling by imbibition. Albumen crystals may occur directly in the cytoplasm ; as, for instance, in the cells poor in starch in the peripheral layers of potatoes, and in chromatophores (Fig. 27). They are sometimes found even in the cell-nucleus. This is particularly the case in the Toothwort (*Lathraea*), and in many Scrophulariaceae and Oleaceae.

B. Inclusions of the Chromatophores

Crystals of albumen and of pigments have already been mentioned as occurring in chromatophores (Fig. 27), but the most important inclusion is STARCH (^{26}). The chloroplasts in plants exposed to the light almost always contain starch-grains (Fig. 15). These grains of starch found in the chloroplasts are formed in large numbers, but as they are continually dissolving, always remain small. Large starch-grains are found only in the reservoirs of reserve material, where starch is formed from the deposited products of previous assimilation. Such starch is termed RESERVE STARCH, in contrast to the ASSIMILATION STARCH formed in the chloroplasts. It also only arises in chromatophores, in this case the LEUCOPLASTS or starch-builders (p. 19) which form it from sugar, even in the absence of light.

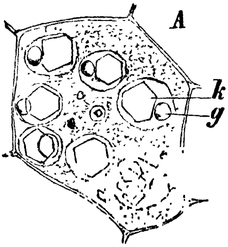

FIG. 22.— Cell from the endosperm of *Ricinus communis*, in water; *k*, albumen crystals; *g*, globoid. (× 540. After STRASBURGER.)

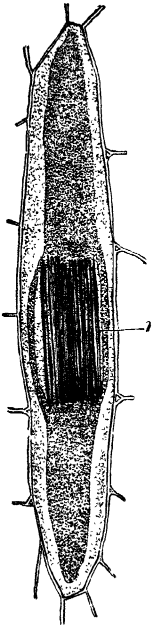

FIG. 21.—Cell from the cortex of *Dracaena*, filled with mucilaginous matter and containing a bundle of raphides, *r*. (× 160. After SCHENCK.)

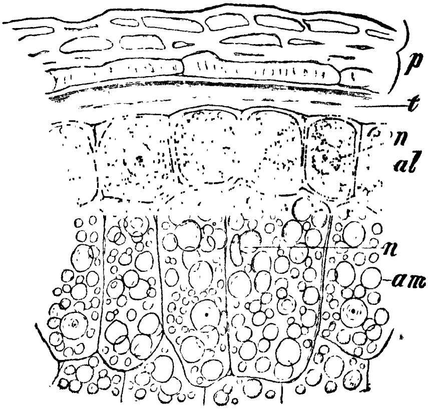

FIG. 23.—Part of a section of a grain of wheat, *Triticum vulgare*. *p*, Pericarp; *t*, seed coat, internal to which is the endosperm; *al*, aleurone grains; *am*, starch grains; *n*, cell nucleus. (× 240. After STRASBURGER.)

All starch used for economic purposes is reserve starch. The amount of starch contained in reservoirs of reserve material is often considerable; in the case of potatoes 20 per cent of their whole weight is reserve starch, and in wheat the proportion of starch is as high as 70 per cent. The starch flour of economic use is derived by washing out the starch from such reservoirs of reserve starch. In the preparation of ordinary flour, on the contrary, the cell-walls and protoplasts of the tissues containing the starch are retained in the process of milling.

The reserve starch consists of flat or roundish (oval or circular) grains, differing in size in different plants. A comparison of the accompanying figures (Figs. 24-26), all equally magnified, will give an idea of the varying size of the starch-grains of different plants. The size of starch-grains varies, in fact, from 0·002 mm. to 0·170 mm. Starch-grains 0·170 mm. in size may be seen even with the naked eye, as minute bright bodies. The starch-grains stored as reserve material in potatoes are comparatively large, attaining an average size of 0·09 mm. As shown in the above figure (Fig. 24), they are plainly stratified. The stratification is due to the varying densities of the successive layers; thicker denser layers—which appear clear by transmitted light—alternate with thinner less dense layers—which appear dark. They are excentric in structure, since the organic centre, about which the different layers are laid down, does not correspond with the centre of the grain but is nearer to one margin. The starch-grains of the leguminous plants and cereals, on the other hand, are concentric, and the nucleus of their formation is in the centre of the grain. The starch-grains of the kidney bean, *Phaseolus vulgaris* (Fig. 25), have the shape of

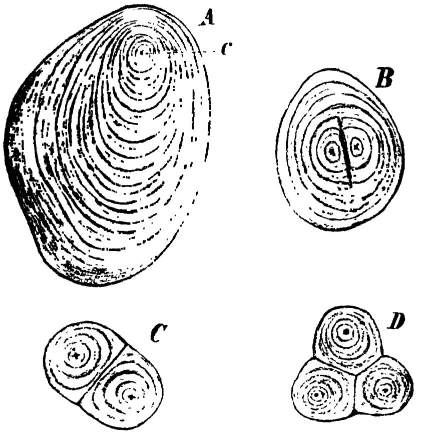

FIG. 24.—Starch-grains from a potato. *A*, simple; *B*, half-compound; *C* and *D*, compound starch-grains; *c*, organic centre of the starch-grains. (× 540. After STRASBURGER.)

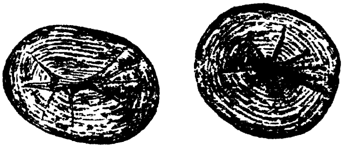

FIG. 25.—Starch-grains from the cotyledons of *Phaseolus*. (× 540. After STRASBURGER.)

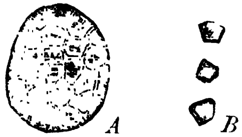

FIG. 26.—Starch-grains of the oat, *Avena sativa*. *A*, Compound grain; *B*, isolated component grains of a compound grain. (× 540. After STRASBURGER.)

flattened spheres or ellipsoids; they show a distinct stratification, and are crossed by fissures radiating from the centre. The disc-shaped starch-grains of wheat are of two very different sizes, the larger lens-shaped and indistinctly stratified, and the smaller minute spheres. In addition to the simple starch-grains so far described, half-compound and compound starch-grains are often found. Grains of the former kind are made up of two or more individual grains, surrounded by a zone of peripheral layers enveloping them in common. The compound grains consist merely of an aggregate of individual grains unprovided with any common enveloping layers. Both half-compound (Fig. 24 *B*) and compound starch-grains (Fig. 24, *C*, *D*) occur in potatoes, together with simple grains. In oats (Fig. 26) and rice, all the starch-grains are compound. The compound starch-grains of rice consist of from 4 to 100 single grains; those of the oat of about 300, and those of *Spinacia glabra* sometimes of over 30,000. Starch-grains have thus distinctive forms in different plants.

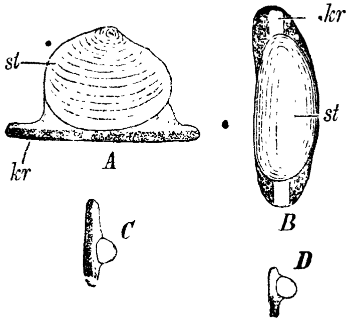

FIG. 27.—Leucoplasts from an aerial tuber of the orchid *Phajus*. *A*, *C*, *D*, viewed from the side; *B*, viewed from above; *st*, starch grain; *kr*, proteid crystal. (× 540. After STRASBURGER.)

The structure of starch-grains becomes intelligible in the light of their mode of formation. If the starch-grain is uniformly surrounded by the leucoplast during its formation, it grows uniformly on all sides and is symmetrical about its centre. If the formation of a starch-grain begins near the periphery of a leucoplast, the grain will grow more rapidly on the side on which the main mass of the leucoplast is present, and the starch-grain thus becomes excentric (Fig. 27). Should, however, several starch-grains commence to form at the same time in one leucoplast, they become crowded together and form a compound starch-grain, which, if additional starchy layers are laid down, gives rise to a half-compound grain.

Starch-grains are composed of a carbohydrate with the formula $(C_6H_{10}O_5)_n$. When it is to be employed further in the metabolism of the plant, starch is again transformed into sugar (maltose) by the action of an enzyme called DIASTASE.

Starch-grains may be regarded as crystalline sphaero-crystals, which are built up of radially arranged, needle-shaped crystals of α- and β-amylose. With polarised light they show, like inorganic sphaerites, and those of inulin (p. 27), a dark cross, an appearance depending on the doubly-refractive nature of the elements of the starch-grain. Röntgen rays also demonstrate the starch-grains as constructed of rhombic crystallites. The stratification is the expression of differences in form and abundance of the crystalline needles in the successive layers.

Starch-grains are as a rule coloured, first blue and then almost black, by a watery solution of iodine. They are easily swollen at ordinary temperatures in solutions of potash or soda and by chloral hydrate. They also swell and form a paste in water at 60°-80° C. They dissolve, *i.e.* are transformed into sugar without previous swelling, in concentrated sulphuric acid. Heated without the addition of water, or roasted, the starch is transformed into an imperfectly known substance that is soluble in water.

IV. THE CELL-WALL (27)

Each protoplast in plants is as a rule enclosed by a firm investment called the cell-wall. This is formed on the outside of the protoplast and is not itself regarded as living. Many plants commence their development as naked protoplasts, *e.g.* swarm-spores or egg-cells. These cells, before developing further and dividing, secrete a thin cell-wall clothing the surface. In cell-division, as has already been described, a partition wall is usually formed between the new cells so that each protoplast remains enclosed by a cell-wall.

The form of cells is usually dependent on the cell-wall, for the naked protoplast behaves like a fluid drop. The relatively small and uniformly shaped meristematic cells attain their ultimate size and special shapes by the **growth in surface** of their walls. This growth is sometimes the same all round, and at other times is limited to the tip or an angle of the cell, to a girdle-like zone, or some other circumscribed region. It comes about as a result of the stretching of the wall, or else by the insertion of new material between the particles of the existing wall (GROWTH BY INTUSSUSCEPTION).

The cell-wall serves to protect and also to give rigidity to the protoplast. This is attained both by the tension of the membrane (TURGOR, cf. p. 219) and by the **growth in thickness** of the cell-wall. While the ultimate form of the cell involves growth in surface of the cell-wall, it is by the growth in thickness that the latter attains its characteristic structure. The growth in thickness, which commences during the growth in surface of the wall, continues after this is complete. It is usually effected by APPOSITION, *i.e.* the deposition of material by the protoplasm on the already existing wall in the form of new layers or lamellae. In this way a concentric stratification of the cell-wall arises (Fig. 29). In the thickened wall, thicker, denser lamellae alternate with thinner and less dense layers, which are often not only richer in water but chemically different from the denser layers. The latter are more highly refractive and appear brighter. In many apparently homogeneous cell-walls, such stratification can be recognised after swelling has been brought about by treatment with strong acids or alkalies.

Not uncommonly growth in thickness also depends on the introduction of new material into the existing wall (intussusception).

In many cells the whole extent of the wall is thickened with the exception of small circular, elliptical, or spindle-shaped areas which form the PITS. These appear in the thickened wall as depressions (Fig. 28) or tubular canals (Fig. 29), closed at one end, as a rule the outer, by the unthickened portion of the cell-wall which forms the pit membrane (Fig. 28 *B*). Sometimes with the increase in the thickness of the wall the canals of several pits unite forming BRANCHED PITS. Such branched pits have usually very narrow canals and occur for the most part in extremely thick and hard cell-walls as, for instance, those of sclerotic cells or sclereides (Fig. 29).

In other cells the greater part of the wall is only slightly thickened, while narrowly circumscribed portions thicken greatly and assume the form of projections, warts, simple or branched pegs (Fig. 30), spines, ridges, bands, or a network (Figs. 64, 65). Such thickenings may form either on the outside (centrifugal) or on the inner surface of the wall (centripetal). Small projections often occur on hairs, while the thickenings of spores and pollen grains (Fig. 31) are characteristic.

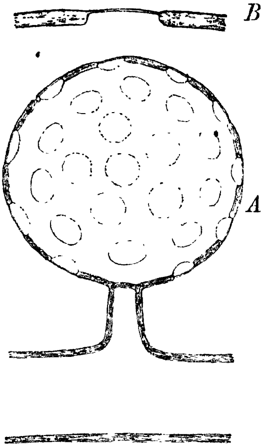

FIG. 28.—*A*, Spherical stalked cell of *Saprolegnia* with circular pits in the wall. *B*, One pit of this in optical section more highly magnified.

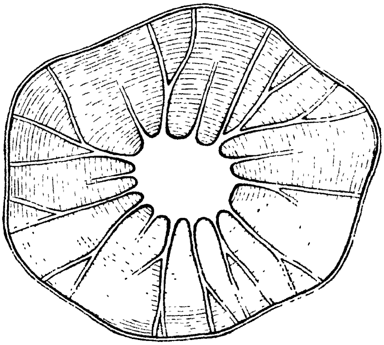

FIG. 29.—Sclerotic cell from the shell of a walnut showing stratification of the wall and branched pits. The canals of some of these pass obliquely out of the plane of section. (ROTHERT, after REINKE.)

A very peculiar form of thickening, with calcium carbonate deposited in it and localised to one small region of the wall, is seen in the CYSTOLITH which forms a stalked body, hanging in the cell like a bunch of grapes (*Ficus elastica*, Fig. 32).

Centrifugal thickening of the wall is frequently brought about by intussusception. This can take place at some distance from the protoplasm and be associated with chemical and structural differentiation of the cell-wall, which thus behaves almost as if it were a living structure. The centrifugal thickening of the walls of cells which have arisen by free cell formation (*e.g.* ascospores) is effected by the periplasm from which the cells have been cut out (cf. p. 25). Similarly the thickenings of many pollen grains and spores are deposited from without by the protoplasm of the tapetal cells which line the cavities in which they are developed. The protoplasts of the tapetum fuse to a periplasmodium surrounding the young spores or pollen grains ([28]).

In some cases fine striae, running obliquely to the longitudinal axis of the cell, are apparent when the thickening layers are viewed from the surface (Fig. 33). This STRIATION depends either on a distinction in the individual thickening layers of regions of different density, the denser frequently projecting into the cell cavity, or (in many Algae such as *Cladophora*) on a wave-like folding of the lamellae. If the wall is distinctly stratified the striae in successive thickening layers are usually inclined in opposite directions (Fig. 33).

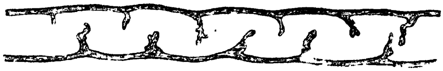

FIG. 30.—Portion of a tubular rhizoid of *Marchantia* with local peg-like thickenings of the wall. (× 240.)

Chemical Nature of the Cell Wall ([29]).—In living cells the cell-wall is always permeated by water and swollen, but shrinks correspondingly when the water is more or less completely removed. The lamellae of the wall consist of CARBOHYDRATES, in the main of CELLULOSES, but also of HEMICELLULOSES or PENTOSANES, and as a rule of several of these substances.

The cell-walls thus never consist of pure cellulose. The celluloses occur in the walls of all plants with the exception of many fungi; they are polysaccharides, the composition of which is expressed by the formula $(C_6H_{10}O_5)_n$. They stain blue with chlor-zinc-iodide solution but not with iodine alone. This reaction holds for many hemicelluloses which are also polysaccharides. The cell-wall nearly always contains other substances in considerable amount, some of which are stained other colours than blue by chlor-zinc-iodide. The PECTIC SUBSTANCES are especially important; these take a yellow colour with this reagent. It depends on this that many "cellulose walls" do not give a pure blue with chlor-zinc-iodide but stain violet, brownish violet, or brown. CHITIN, formerly regarded as peculiar to the animal body, is present in the walls of most Fungi.

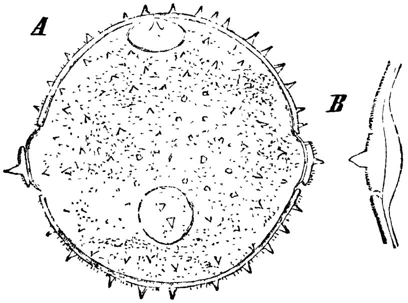

FIG. 31.—*A*, Pollen-grain of *Cucurbita Pepo* in surface view, and partly in optical section, rendered transparent by treating with oil of lemons. (× 240.) *B*, Part of transverse section of pollen grain. (× 540. After STRASBURGER.)

The CELLULOSES are insoluble in dilute acids and alkalies; even concentrated potash solution does not dissolve them. They are, on the other hand, soluble in ammonia-oxide of copper, by concentrated sulphuric acid after conversion into dextrose, and by concentrated hydrochloric acid. They are further acted on by the enzyme cellulase and transformed into glucose, with the dissaccharide cellobiose as an intermediate product. After treatment with sulphuric or phosphoric acid a watery solution of iodine will colour them blue, and a similar reaction is obtained by the simultaneous action of a concentrated solution of certain salts, such as zinc-chloride or aluminium-chloride, and of iodine. Accordingly chlor-zinc-iodide, on account of the blue or violet colour imparted by it, is one of the most convenient tests for cellulose. The name of HEMICELLULOSES is given to a series of substances which are nearly related to the celluloses, but are transformed by even dilute acids into soluble sugars other than dextrose (*e.g.* mannose, galactose). Mucilaginous cell-walls and those consisting of reserve-cellulose are specially rich in hemicelluloses (cf. p. 41). They are often insoluble in ammonia-oxide of copper. As the celluloses are polysaccharides with large molecules produced from hexoses ($C_6H_{12}O_6$), the pentosanes $(C_5H_8O_4)_n$ are corresponding condensation products of pentoses ($C_5H_{10}O_5$) such as arabinose and xylose. The PECTINS (30) are characterised by the ease with which they dissolve in alkalis after previous treatment with dilute acids. In contrast to cellulose, they stain deeply with safranin and methylene blue. The pectins are complex compounds in which monohexoses, pentosane, acetic acid, and in addition methyl alcohol behaving as an ester and calcium and magnesium behaving as salts, are united to tetragalacturic acid ($C_{24}H_{32}O_{24}$, a condensation product of galacturic acid $C_6H_{10}O_7$). It is the presence of pectins that determines the formation of gelatinous material from decoctions of fruits.

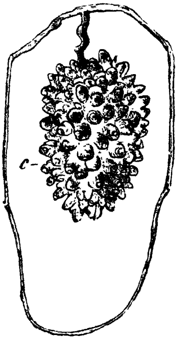

FIG. 32.—Cell of *Ficus elastica* containing a cystolith, c. (× 240. After SCHENCK.)

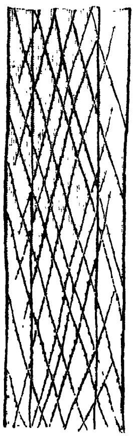

FIG. 33.—Part of a sclerenchymatous fibre from *Vinca*, in surface view. (× 500. After STRASBURGER.)

CHITIN is acetyl-glycosamine ($C_{32}H_{54}O_{21}N_4$).

The cell-wall frequently undergoes chemical changes of various kinds during the life of the cell; sometimes layers already deposited change, in other cases the newly deposited layers are different from those first formed. These transformations stand in the closest relation to the requirements of the plant to which the cells contribute. As regards "cellulose walls," these in young cells are less elastic but relatively more extensible than in older cells; this is advantageous in relation to the active growth in length of young parts. Such walls offer little resistance to the diffusion of water and dissolved substances.

Cellulose walls not infrequently become MUCILAGINOUS, their substance being transformed into a gelatinous or mucilaginous mass which swells greatly in water. Frequently cell-walls undergo LIGNIFICA-

TION, SUBERISATION, or CUTINISATION. Lignification diminishes the extensibility of the cells considerably and increases their rigidity, without lessening the permeability of the wall to water and dissolved substances. Corky and cutinised walls, on the other hand, are relatively impermeable to water and gases, and greatly diminish evaporation.

LIGNIFICATION depends on the introduction into the carbohydrate layers of the cell-wall of lignines. The chemical composition of these is little understood, but benzole derivatives and pentosans enter into this. The innermost layers of the wall of lignified cells consist, however, in many cases of cellulose. Characteristic reactions for lignin are a yellow colour with acid aniline sulphate, and a red colour with phloroglucin and hydrochloric acid. These reactions depend on aromatic substances present in the lignified wall. With chlor-zinc-iodide lignified walls stain yellow, not blue. The lignifying substances can be separated from the walls by prolonged boiling in solutions of calcium bisulphite or caustic soda, under pressure. Only the cellulose lamellae remain and form a source of artificial cellulose. The action of Eau de Javelle on microscopical sections is similar.

SUBERISATION is as a rule limited to the middle thickening layers of a cell-wall. The corky lamellae consist of SUBERIN only and thus contain no carbohydrate. CUTINISATION is closely related to suberisation but not identical. It consists in a secondary deposit of CUTIN on a cellulose wall, or its introduction into the substance of the wall. No sharp distinction can be drawn between cutin and suberin. Both are coloured brownish yellow by chlor-zinc-iodide and take a nearly identical yellow colour with potash; they stain red with sudan-glycerine and are both insoluble in concentrated sulphuric acid or ammonia-oxide of copper. Cutin, however, resists the action of potash better. Both cutin and suberin behave differently to reagents according to their special mode of origin. According to VAN WISSELINGH (31) suberin is a fatty substance which is composed of glycerine esters and other compound esters of phellonic, suberic, and others of the higher fatty acids; the phellonic acid is wanting in the more complex cutin.

In old cell-walls inorganic substances often accumulate in considerable amount. Silicic acid is frequent, calcium carbonate less common, while organic salts such as calcium oxalate also occur. CALCIUM CARBONATE occurs in the walls of certain plants, *e.g.* of most Characeae, in such amount that they become rigid and brittle. SILICIC ACID is present in the peripheral cell-walls of grasses, horse-tails, and many other plants (*e.g.* of the unicellular diatoms), and makes them more rigid. CALCIUM OXALATE when present is usually in the form of crystals.

The cell-walls are frequently coloured dark by derivatives of tannins, and thus, as in seed-coats and in the old wood, are protected against decay. The pigments belonging to the flavone group which occur in the technically valuable woods are also localised in the cell-walls.

Solid cell-walls may undergo a transformation into GUM, as in the gummosis of wood. In species of *Prunus* and *Citrus* the thickening layers of the cell-wall become swollen one after another in this process, and ultimately the cell contents are involved in the change. The gum is chemically similar to mucilage (cf. p. 36).

Spectroscopic examination with Röntgen rays has shown that cellulose walls, in the same way as starch-grains, *have a crystalline structure. They consist of rhombic crystallites which are placed with their main axes oblique to the longitudinal axis of the cell* (32).

SECTION II

HISTOLOGY (33)

I. THE FORMATION OF TISSUES

A. The Idea and Significance of Cellular Tissues

Every close association of protoplasts enclosed in cell-walls is termed a tissue.

Only the lowest organisms are composed of a single uninucleate or multinucleate protoplast and are thus unicellular throughout their life. Usually the body of a plant is multicellular, consisting of many protoplasts separated by cell-walls and thus forming a tissue. The attainment of large size and more complex external organisation is as a rule associated with such a structure. There are, it is true, certain Algae (Siphoneae) (Fig. 343) which are externally highly organised, while they consist internally of a single multinucleate protoplast. These may be contrasted as non-cellular organisms with the ordinary cellular plant, to the construction of which they form an exception. The formation of a cellular tissue is of the greatest importance in the development of more highly organised plants in enabling a division of labour to be effected in the protoplasm of the body. The division of the protoplasm into numerous protoplasts provides elementary parts which can take over different duties. It further greatly increases the surface of the protoplasm. The cell-walls separating the protoplasts isolate the latter more or less, while at the same time increasing the cohesion and the internal rigidity of the whole body formed of the numerous soft protoplasts.

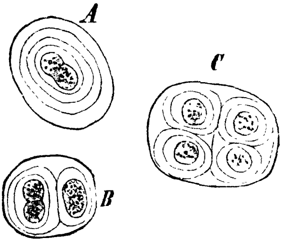

FIG. 34.—*Gloeocapsa polydermatica*. *A*, Single cell; *B*, *C*, divided. (× 540. After STRASBURGER.)

A very imperfect tissue formation is found in those organisms the cells of which separate from one another at each division, but remain connected by the mucilage derived from the swollen cell-walls. Such unions of more or less independent cells that have had a common origin may be termed cell-families or cell-colonies. The Schizophyceae, to which group *Gloeocapsa* (Fig. 34) belongs, and the orders of the Volvocales and Protococcales among the Green Algae afford numerous examples, and the descriptions in the special part should be consulted. In the cell-filaments and cell-surfaces of those lower Algae in which the cells are all equivalent but are united together, the characters of a definite tissue begin to make their appearance. With the increasing number of cells composing the organism we get a contrast between base and apex and the appearance of a growing point, and also progressive division of labour among the cells.

B. Origin of Tissues

The origin of vegetable tissues is, in general, attributable to cell-division. In *Hydrodictyon* among the Algae a tissue is formed by the apposition of free cells. In the Fungi and Siphoneae a tissue arises through the interweaving of tubular cells or cell-filaments (plectenchyma, Fig. 36). In such cases, where the filaments are so closely interwoven as to form a compact mass of cells, the tissue thus formed has the same appearance as the tissues of higher plants (Fig. 35). The mutual interdependence of the cells of such a tissue may even be manifested by the pits corresponding in position on the opposite sides of the walls resulting from the intimate union of the separate cells.

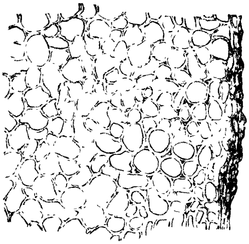

FIG. 35.—Transverse section of the sclerotium of *Claviceps purpurea*. (× 300. After SCHENCK.)

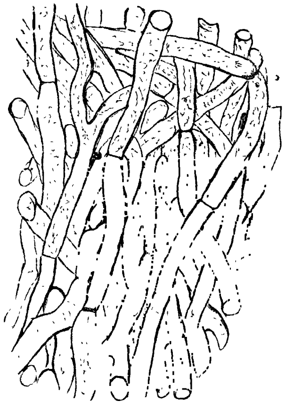

FIG. 36.—Longitudinal section of the stalk of the fructification of *Boletus edulis*. (× 300. After SCHENCK.)

C. The Cell Walls in the Tissues

When sections of vegetable tissues are examined under a low magnification attention is attracted mainly or only by the cell-walls. These appear to form a network of threads something like a woven tissue, and the name takes its origin from this inaccurate comparison.

1. Stratification.—All the septa arising in the course of cell-divisions in tissues are at first very thin and simple lamellae, common to the two cells the protoplasts of which they separate. The cell-wall never remains in this condition. Even in meristematic cells it becomes thickened as the membrane grows in surface extent. Thickening only ceases long after the cell has reached its ultimate size. It varies according to the functions taken over by the cell as part of a permanent tissue, especially thick walls being found in cells which contribute to the mechanical rigidity of the plant (Fig. 37). As a rule the thickening of a partition wall is effected by the two adjoining protoplasts depositing new lamellae on both sides of the original thin septum (Figs. 37, 38, 59). The thickening may thus be equal or unequal on the two sides and each protoplast comes to have its own surrounding layers. The common middle region of the wall is called the MIDDLE LAMELLA (Fig. 37 *m*). It is as a rule very thin, only widening out somewhat at the angles where several walls meet (Fig. 68 *Cm**), and consists mainly of pectic substances containing calcium; it is relatively easily dissolved. In lignified and suberised tissues the middle lamella is frequently lignified.

In soft tissues even boiling in water may swell the middle lamella and so separate the cells (*e.g.* many kinds of potatoes). In ripe fruits this separation occurs naturally. Treatment with SCHULZE's macerating fluid (potassium chlorate and nitric acid) or with concentrated solution of ammonia will separate other cells by destroying the middle lamella. The macerating fluid will thus isolate the elements of wood. There are also certain Bacteria which ferment pectic substances by means of the enzyme, pectinase, and thus bring about the separation of the cells; in this way the mechanical cells of Flax are isolated in the process of retting.

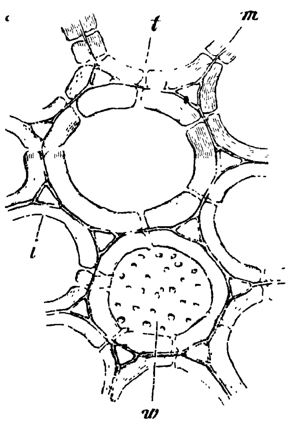

FIG. 37.—Strongly thickened cell from the pith of *Clematis vitalba*. *m*, Middle lamella; *i*, intercellular space; *t*, pit; *w*, pitted cell-wall in surface view. (× 300. After SCHENCK.)

The thickening layers are distinguishable from the middle lamella both by their optical and chemical properties. Since they usually lie equally on both sides of the middle lamella the whole wall acquires a more or less symmetrical construction (Figs. 37, 38, 39, 40, 59) which extends to the pitting.

Three distinct layers can frequently be distinguished in strongly thickened cell-walls, such as those of the wood, a primary, a secondary, and a tertiary thickening layer: these differ in their optical appearance and their chemical composition. The secondary thickening layer is usually the most strongly developed, and forms the chief part of the cell-wall.

Cell-walls which do not adjoin other cells (Figs. 38, 42) and especially the external walls of the plant are, on the other hand, asymmetrically constructed. In such cases thickening layers can only be deposited on the side of the original cell-wall which faces the cavity of the cell.

2. Pitting.—The cell-walls which separate the protoplasts will evidently render difficult the passage of materials from cell to cell in proportion to the thickness of the wall. The life of the organism could not continue without such transport of material. It is therefore necessary that this should not be too greatly hindered by the thickening of the walls that ensures rigidity. The difficulty is met by the formation of pits in the walls between the protoplasts, while pits are as a rule wanting in the free external walls.

The pits, which in greatly thickened walls form canals with circular (Fig. 37 *w*,) or elliptical cross-section, meet accurately, and would form one continuous canal were it not that the unthickened primary wall persists as a pit-membrane (Figs. 37 *t*, 38 *t*).

The openings of narrow elliptical pits into adjoining cells usually appear to cross one another obliquely.

The structure of pits may be very easily seen in the greatly thickened and abundantly pitted cell-walls of the seeds of various Palms (Fig. 40), Liliaceae (*e.g. Ornithogalum*), and other Monocotyledons (Fig. 601). The thickening here consists of a hemicellulose which forms a reserve material in the seed, and at germination is dissolved by an enzyme (cytase). The walls have a gleaming, white appearance, and are so hard that such seeds, *e.g.* of the Palm, *Phytelephas macrocarpa*, are technically known and employed as vegetable ivory.

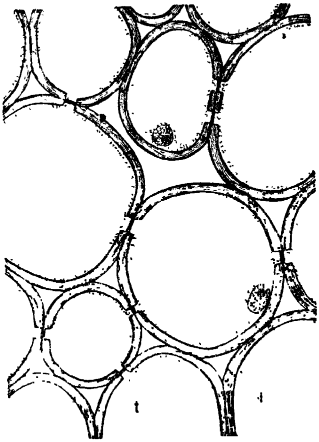

FIG. 38.—Cells from the cortex of the root of *Iris*. *t*, Pits in the stratified cell-wall; *i*, intercellular spaces. (× about 400.)

3. Cell-Fusions.—Rapid transport of substances within the body of the multicellular plant is necessary, for instance from one organ to another, as from the roots to the leaves. The process of diffusion through the cell-walls, even when assisted by the presence of the pits, does not suffice to meet this need. The cavities of many cells, especially those which serve for rapid transport, therefore become continuous by relatively wide openings, so that they form tubular structures or CELL-FUSIONS (cf. pp. 59, 61, 66). Such openings arise singly or in numbers by a solution of the cell-wall substance, especially in the end walls of adjoining cells.

4. Connections of the Protoplasts in Tissues.—The harmonious co-operation of all the living parts of the body, which is such a striking feature of the life of an organism as a whole, would hardly be possible if the protoplasts forming the tissues were completely divided from one another by the cell-walls. It can in fact be shown that the protoplasts of the plant are united together by extremely fine cytoplasmic filaments, which proceed from the boundary layer of the cytoplasm and are known as PLASMODESMS (^{34}). Such filaments are mostly confined to the pit-membrane (Fig. 39 *s*), but may also penetrate the whole thickness of the cell-wall (Fig. 40 *pl*). The existence of these connecting filaments of living substance between the protoplasts confers an organic unity on the whole body of the plant, serving for the conduction both of substances and of stimuli.

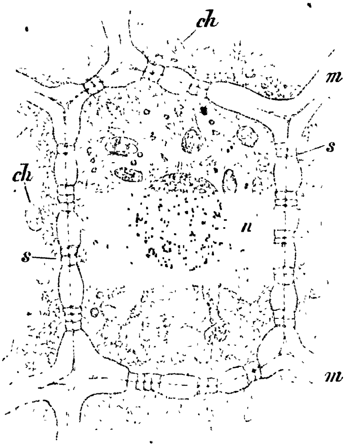

FIG. 39.—A cell from the cortex of the Mistletoe (*Viscum album*); the protoplast has been properly fixed and stained and the wall (*m*) swollen. The pit membranes (*s*) are traversed by connecting threads (plasmodesms); *ch*, chloroplasts; *n*, nucleus. (× 1000. After STRASBURGER.)

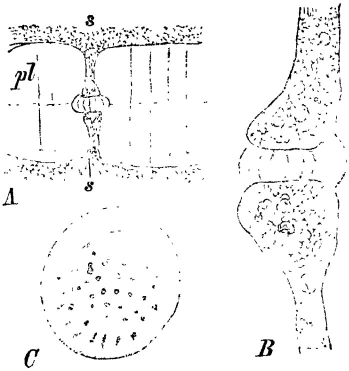

FIG. 40.—*A*, A swollen portion of cell-wall from the endosperm of the Vegetable Ivory Palm (*Phytelephas macrocarpa*). At *s*, *s*, simple pits filled with cytoplasm; in the intervening pit membrane are fine connecting threads (plasmodesms); *pl*, other plasmodesms traversing the whole thickness of the wall. (× 375.) *B*, The contents of two opposed pits and the connecting threads of the pit membrane. (× 1500.) *C*, the opening of a pit and the connecting threads of the pit membrane viewed from the surface. The smaller circle indicates the canal of the pit, while the larger circle is the pit membrane; the dark points on the latter are the plasmodesms. (× 1500 After STRASBURGER.)

5. Formation of Intercellular Spaces and the Ventilation of the Tissues.—Usually as the meristematic cells are transformed into permanent tissue and the cell-walls thicken, the middle lamella splits locally, especially at the angles of the cells. At these points the walls of neighbouring cells separate and INTERCELLULAR SPACES filled with air arise throughout the plant (Figs. 37, 38 *i*). In accordance with their mode of origin the smaller intercellular spaces are triangular or quadrangular in transverse sections. They form a connected system of narrow, branched canals (INTERCELLULAR SYSTEM) which traverse the tissues in all directions. From their mode of origin by the splitting of cell-walls such intercellular spaces are termed SCHIZOGENOUS. Unequal growth of the tissues may lead to the complete isolation of cells or the formation of larger chambers or passages of more or less regular form. Intercellular spaces can also arise by the dissolution or breaking down of cells and are then termed LYSIGENOUS and RHEXIGENOUS respectively. Sometimes spaces, that are in their origin schizogenous, are further enlarged rhexigenously or lysigenously. Whole regions of the tissue may be stretched and broken down by unequal growth. Hollow stems arise rhexigenously. In tissues which have arisen by a weaving together of filaments (Fig. 36) the intercellular spaces are present from the outset.

Intercellular spaces usually contain air and are of great importance for the living cells forming the tissues. A single cell in water or air can obtain at any time the gases, especially oxygen, which are essential to its life from the surrounding medium. The life of the numerous protoplasts in the tissues of a plant requires a supply of oxygen. This introduction and circulation of gases in the tissues is carried out by the system of intercellular spaces.

II. KINDS OF CELLS, TISSUES, AND TISSUE-SYSTEMS

Only in the lower multicellular plants does the tissue consist of equivalent, spherical, polyhedral, and cylindrical cells (cf. *e.g.* Fig. 81), which are similarly able to perform all the vital functions. This tissue may be termed PARENCHYMA. As the division of labour between the protoplasts increases, with increase in size and progressive external organisation, cells or groups of cells acquire diversity in form, structure, and function. There results in the higher plants a segregation of the originally uniform cells into variously constructed kinds of cells, connected, it is true, by intermediate forms. Comparative study of the various organs of a plant, and of all the higher plants, shows that the number of these KINDS OF CELL is limited, and that DEFINITE FORMS OF CELLS RECUR IN THEM ALL.

Similar cells are usually associated in groups which constitute a KIND OF TISSUE. These are distinguished by the form, contents, and the walls of their constituent cellular elements, and each kind of tissue has its special function or functions. More highly organised plants are composed of a number of kinds of tissue, but, as in the case of kinds of cells, this number is small, since they recur in the most diverse plants. It is not uncommon for single cells (idioblasts) or cell-groups of a different structure and content to be found in an otherwise uniform type of tissue.

In the higher plants particular kinds of tissue may occur in considerable amount and extend in unbroken connection for a distance or through the whole plant body. These may often include several associated kinds of tissue and constitute MORPHOLOGICAL TISSUE SYSTEMS. Such compound associations of tissues may be characterised structurally and have different main functions.

In a PHYSIOLOGICAL TISSUE-SYSTEM are grouped together all cells that agree in their main functions, irrespectively of their morphological connection or of their ontogenetic origin. Such physiological systems are thus something quite different from morphological tissue-systems.

The tissue-systems of the more highly organised plants can be divided into two main groups: (1) the meristematic or formative tissues; (2) the mature or permanent tissues.

A. The Formative Tissues

These are also termed MERISTEMS and consist either of relatively small cubical or isodiametric cells, or of prismatic, flattened, or elongated cells with thin walls, abundant protoplasm, large nuclei, and few and small vacuoles (cf. Fig. 2). The numerous cell-divisions that occur in their cells is characteristic. These formative tissues, from which the permanent tissues are developed, are distinguished according to the place and mode of their origin into PRIMARY and SECONDARY MERISTEMS.

1. **Primary Meristems** (35).—These arise by the division of the germ-cell and at first compose the whole embryo. Later they become localised at the growing points of the branches and roots (Figs. 98, 150), where the increase in number of meristematic cells takes place (apical growth).

A short distance behind the growing point the similar cells of the primary meristem begin to grow differently and give rise to strands and layers of variously shaped formative cells, which at first retain the general characters of meristematic cells (Figs. 96, 98, 150). Intercellular spaces, absent in the meristem itself, now arise. At a somewhat greater distance from the growing point the characters of the various permanent tissues make their appearance and become more marked basipetally until the mature structure is attained. In developing from the meristem the cells of the permanent tissue enlarge, separate at places from one another, undergo thickening and chemical alterations of their walls, modify or lose their cell contents, and sometimes fuse by dissolution of the partition walls. In enlarging or elongating the cells may behave independently (Fig. 167), so that the ends of some which elongate greatly push past, or in between, other cells (SLIDING GROWTH) (36).

In this process of tissue-differentiation groups, strands, or layers of cells may retain the meristematic characters and serve as places of origin later for a renewed formation of meristematic and mature tissues. Their power of division may persist throughout the life of the plant.

In many Monocotyledons the basal regions of the internodes remain for a long time meristematic, and serve, in addition to the growing point, as places of production of permanent tissue. In this way the intercalary growth of these and other plants is brought about.

2. **Secondary Meristems** are derived either from the above-mentioned inactive remains of the primary meristem or are newly formed from cells of the permanent tissue, which alter their function and by new cell-divisions are transformed into meristematic cells. Their elements resemble those of the primary meristems, but as a rule have the form of elongated or flattened prisms (Fig. 162). Such secondary meristems, which get the name CAMBIUM, give origin to

cork and to the secondary growth in thickness of woody plants. They form a thin layer of prismatic meristematic cells (Figs. 160, 166) parallel to the surface of the organ at the outside of the cylinder of wood. In the cambium a middle layer of initial cells undergoes continued tangential divisions which cut off daughter-cells to both the inside and outside in the radial direction. These cells after some further divisions are transformed into cells of the permanent tissues.

The new cell-walls arising in the cell-divisions of a meristem are flat and as a rule, though not without exception, placed at right angles to the pre-existing older walls. Walls more or less parallel to the surface of the organ are termed PERICLINAL, and those at right angles to this ANTICLINAL.

B. The Permanent Tissues

The cells of the permanent tissues differ from the meristematic cells in being as a rule larger, with relatively little protoplasm and large vacuoles, and sometimes completely dead. Cell-divisions are not usually taking place in them, and the cell-walls are variously thickened and often chemically altered. The permanent tissue is composed of a variety of kinds of cells and tissues with diverse functions. It is usually provided with intercellular spaces.

The permanent tissues may be classified in various ways. Thus according to their origin primary and secondary permanent tissues may be distinguished arising from the corresponding meristems.

A morphologically useful division of the permanent tissues is obtained when all the differences of the component cells are taken into consideration together.

On examining the tissues of the higher plants comparatively there is found in the first place a tissue which, like that composing the lowest multicellular plants (cf. p. 4[illegible]), consists of cells with living contents and thin cellulose walls, and is capable of performing a diversity of functions; this will be termed PARENCHYMA. Other tissues may be sharply distinguished from this parenchyma by peculiarities of structure and special functions. The most striking tissues in the light of their main functions are the BOUNDARY TISSUE, the MECHANICAL TISSUE, and the CONDUCTING TISSUE. The PARENCHYMATOUS SYSTEM, the EPIDERMAL SYSTEM, the MECHANICAL SYSTEM, and the CONDUCTING SYSTEM correspond on the whole to these tissues. In addition the SECRETORY TISSUE and GLANDULAR TISSUE may be recognised.

The permanent tissues are frequently divided into epidermis, vascular bundles, and ground tissue.

It was formerly usual to take the dimensions of the cells into special consideration, and on this ground PARENCHYMA and PROSENCHYMA were distinguished. By parenchyma was understood a tissue the cells of which were isodiametric or, if elongated in one direction, were separated by transverse walls. Prosenchyma was a tissue the elongated cells of which were spindle-shaped and pointed at both ends. These two groups do not, however, suffice to give a survey of the variety of kinds of tissues, and the underlying conceptions are out of date.

1. Parenchyma. Parenchymatous System.—The parenchyma cell is characteristic of this type of tissue. It may be isodiametric or elongated and of various shapes, and possesses the following further characters (cf. Figs. 3 *B*, 38, 39). The cell-wall, which as a rule consists of cellulose, is only moderately thickened and provided with simple round or elliptical pits; it thus facilitates the diffusion of substances from cell to cell. Living protoplasm is usually present, and the large vacuole may contain a considerable amount of nutritive material. The chromatophores, which have the form of chloroplasts or leucoplasts, often contain starch. Parenchyma is usually traversed by a ventilating system of intercellular spaces. Parenchyma may form part of other primary or secondary tissues and serves a variety of functions. The most important vital processes of the full-grown plant take place in it, such as the preparation, conduction, and storage of nutritive materials, water storage, and the process of respiration. The presence of abundant cell-sap contributes to the maintenance of the general rigidity of the plant body. The structural differences between parenchyma cells are relatively slight when the multiplicity of functions they perform are considered. When the cells have numerous chloroplasts they are spoken of as ASSIMILATORY PARENCHYMA (Fig. 8) in reference to their main function of forming organic substance from carbon-dioxide. The parenchyma of the subaerial parts of plants is often of this nature so far in as light can penetrate, while the deeper tissues are colourless. The term STORAGE TISSUE is applied when these cells are rich in organic contents such as sugar, starch, fatty oils or proteids, or have hemicelluloses accumulated in the thickened walls; these substances are stored against future use in the metabolism (Figs. 22, 23, 600). WATER-STORAGE PARENCHYMA as a rule consists of large thin-walled cells with little protoplasm but abundant cell-sap that is somewhat mucilaginous; these cells diminish in size on losing water. Conduction of organic food-materials, especially of carbohydrates, takes place in parenchymatous cells, which are elongated in the main direction of transport to facilitate this function. Such CONDUCTING PARENCHYMA often forms a sheath, without intercellular spaces, around other masses of tissue. Parenchyma which has large intercellular spaces, serving for ventilation or the storage of gases, is termed AERENCHYMA.

2. Boundary Tissues.—In the case of the multicellular tissues composing the bodies of land-plants the whole body or particular tissues may require protection against excessive loss of water, mechanical injury, excessive heat (37), and frequently against the loss of diffusible substances. This function is carried out by cells which have certain peculiarities of structure and are often arranged in sheathing layers. In this way another group of tissues can be distinguished, the main elements of which are the EPIDERMAL CELLS and the suberised or CORK CELLS. The epidermis together with some other types of cell form the epidermal system.

(a) Epidermal System. 1. EPIDERMIS.—This is derived from the superficial layer of the primary meristem (the dermatogen, cf. p. 82) and is thus one of the primary permanent tissues. It encloses the plant-body as a protective investment while permitting exchange of materials with the environment. The epidermis is typically a single layer (Fig. 43 *B*) of tabular or more elongated living cells, without intercellular spaces between them. The lateral walls are often undulated or toothed, (Fig. 41) which increases the firmness of the union of the cells. In transverse section the cells are of uniform depth and are rectangular or lens-shaped. The protoplasts of the epidermal cells are commonly reduced to thin layers lining the walls and enclosing large vacuoles filled with colourless or coloured cell-sap. The epidermis of the parts exposed to light in most Ferns and in many shade-loving Phanerogams is provided with chlorophyll and takes part in assimilation. More usually chlorophyll is absent from the epidermis.

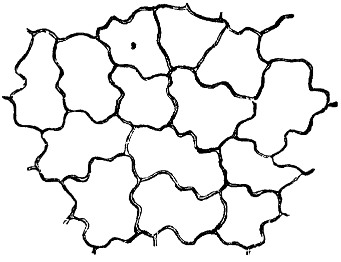

FIG. 41.—Surface view of the epidermis from the upper side of a leaf of *Mercurialis perennis*. (× 300. After H. SCHENCK.)

The outer walls of the epidermal cells of all subaerial parts of the plant, which last for a considerable time, are thickened. In this respect they contrast with the epidermal cells of the more fugitive petals and of submerged and subterranean parts. This holds especially for roots in which the epidermis has very different functions, such as the absorption of water and salts. The thickening of the outer walls results from the apposition of cellulose layers, the outer of which usually, but not always, become more or less strongly cutinised (Fig. 183).

The outer walls of the epidermal cells, whether thickened or not, except in the case of those forming the surface of subterranean organs and especially roots, are covered by a thin continuous cutinised film called the CUTICLE. This is formed on the primary walls of the epidermal cells. The cuticle is often somewhat folded and in surface view appears striated. The cuticle and the cutinised layers of the wall are only with difficulty permeable to water and gases, and prevent the injurious loss of water by evaporation. The thickening also increases the mechanical rigidity of the epidermal cells. On the other hand, the absence of cuticle from the root facilitates the absorption of water and salts from the soil.

Deposits of WAX are also present in the cutinised layers of the epidermis and render it even less permeable by water (38). Consequently water will flow off the epidermis without wetting it. The wax is sometimes spread over the surface of the cuticle as a wax covering. This is the case in such fruits as plums and grapes, on which it forms the so-called bloom. The wax coverings may consist of grains, small rods (Fig. 42), or crusts.

The wax of plants is soluble in ether or in hot alcohol. Like the suberins and cutins it consists of fatty acid esters of glycerine mixed with free fatty acids and esters of fatty acids of other alcohols.

The epidermis may not only protect the more internal tissues from loss of water by hindering evaporation, but also by serving as a place of storage of water. The unthickened lateral walls of these cells become folded as the water is withdrawn from the cavity and stretch when the cell becomes again filled. Such an epidermis is frequently also composed of several layers of cells.

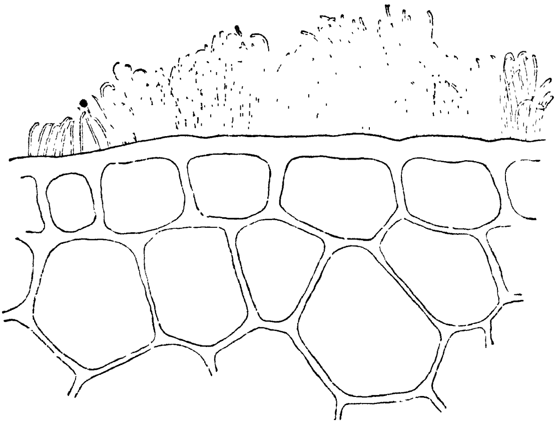

FIG. 42.—Transverse section of a node of the sugar-cane, *Saccharum officinarum*, showing wax incrustation in the form of small rods. (× 540. After STRASBURGER.)

The mechanical strength of the outer walls of epidermal cells is increased in some plants by the deposition of calcium carbonate or of silicic acid. In the case of *Equisetum* the silicification is so great that the tissues are used in polishing tin-ware.

The epidermis of fruits, and particularly of seeds, exhibits a considerable variety of modifications in its mode of thickening and in the relations the thickening layers bear to one another. In addition to protecting and enclosing the internal parts, the epidermis has often to provide for the dissemination and permanent lodgment of the fruits and seeds. (39)

2. STOMATAL APPARATUS (40).—The presence of stomata in the epidermis is characteristic of most parts of the more highly organised plants that are exposed to the air. Each stoma is an intercellular passage or pore bounded by a pair of curved, elliptical or half-moon-

shaped cells called GUARD CELLS. The pore and guard cells together constitute the STOMA or STOMATAL APPARATUS (Figs. 43 *A*, 44). The largest stomata are found in grasses; thus in the wheat they measure 0·079 mm. in length by 0·039 mm. in breadth, while the pore itself is 0·038 mm. by 0·007 mm. Stomata never occur in the epidermis of the root.

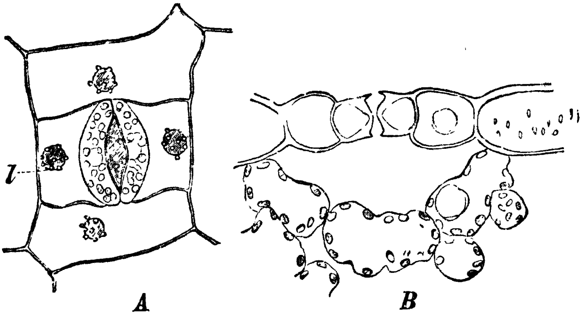

FIG. 43.—Epidermis from the under side of a leaf of *Tradescantia virginica*. *A*, In surface view. *B*, in transverse section; *l*, colourless rudiments of chromatophores surrounding the nucleus. (× 240. After STRASBURGER.)

The PORE interrupts the continuity of the epidermis. It is an air-filled intercellular space opening below the epidermis into a large intercellular space (Fig. 43 *B*), which is spoken of as the respiratory cavity although it has nothing to do with respiration. This cavity is in communication with the intercellular spaces of the parenchyma. The stomata are of great importance to the plant, for they place the system of intercellular spaces, which serves to ventilate the tissues, in communication with the external atmosphere. This connection is necessary on account of the difficulty with which gases pass across the epidermis in order to renew the air in the intercellular spaces, and especially to replace the carbon-dioxide as this is used up. On the other hand, oxygen, which forms a considerable proportion of the air, can usually penetrate into the plant in sufficient quantity through the cuticle and the epidermal cells.

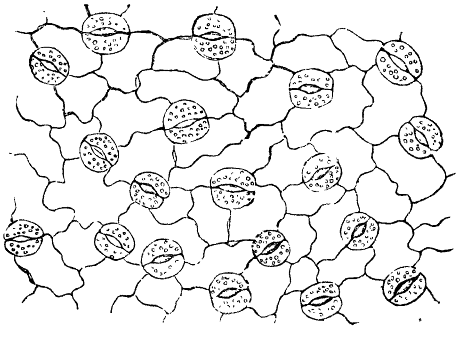

FIG. 44.—Epidermis with stomata from the lower surface of the leaf of *Helleborus niger*. (× 120. After STRASBURGER.)

The GUARD CELLS always contain chlorophyll and are characterised both by their shape and the manner in which their walls are thickened. This is best shown in transverse sections (Figs. 43 *B*, 45 *B*). There are usually an upper and a lower thickened band on the side of the guard cell which faces the pore, the portion of the wall between and the rest of the wall of the guard cell being relatively thin (Fig. 43 *B*). This structure stands in relation to the changes in form of the guard cells by means of which the size of the pore is varied. The pore is closed by a diminution of the curvature of the guard cells when there is danger of too great escape of moisture; while it is widely opened by increase in the volume of the guard cells, and consequently of their curvature, at other times. The stomata regulate the gaseous exchange and the transpiration.

As the transverse section in Fig. 43 *B* shows, the thickening ridges project both above and below the pore. There is thus an anterior chamber and a posterior chamber in relation to the narrow region of the actual passage. The thickened outer walls of the epidermal cells immediately adjoining the guard cells often have a thinner portion, which acts as a kind of hinge and enables the changes in shape of the guard cells to be effected without hindrance from the surrounding cells (cf. Fig. 45 *B*). The guard cells, as is seen in Fig. 43 *A*, are often surrounded by special cells called SUBSIDIARY CELLS; these may be less thickened or shallower than the other epidermal cells.

Differences are found in the construction of the guard cells and in the mechanism of opening and closure of the stoma which depends upon this. Two main types of stoma may be distinguished, but they are connected by intermediate forms. In the first the change in form of the guard cells takes place mainly in the tangential direction, parallel to the epidermal surface; in the second in the radial direction at right angles to the surface. TYPE I.—According to the form of the guard cells the pore is opened in various ways. (*a*) The type of the Amaryllidaceae (Fig. 45) is found in the majority of Monocotyledons and Dicotyledons. The dorsal wall of each guard cell (Fig. 45 *B*) is unthickened, while the ventral wall (towards the pore) is thickened and usually shows the upper and lower thickening bands. When the cell becomes turgid the thin dorsal wall is more stretched than the thickened wall, and the cell, which in the flaccid condition was almost straight, becomes curved in the tangential plane to a semilunar shape. (*b*) The type of the Gramineae (Fig. 46) is met with in the Gramineae and Cyperaceae. The guard cells are dumb-bell-shaped; the widened ends being thin-walled, while the narrower middle region has both the outer and inner walls strongly thickened (Fig. 46 *B*). When the turgor increases the stiff middle portions of the guard cells are separated from one another by the expansion of the oval thin-walled ends of the cells. TYPE II.—*Mnium*-type (Fig. 47) is found in some Mosses and Ferns. In this the ventral walls of the guard cells are thin while the dorsal walls are thickened. When the turgor of the guard cell increases, the outer and inner walls are separated from one another, thus lessening the projection inwards of the ventral wall and opening the pore. The position of the dorsal wall remains unchanged. A transition between TYPES I. and II. is afforded by the stomatal apparatus of *Helleborus* (cf. Fig. 235) in which the guard cells become semilunar on stretching of the thin dorsal wall, while at the same time the thickened outer and inner walls are separated. The somewhat different Conifer-type may be mentioned along with this.

The stomata are often formed by the division of a young epidermal cell into two cells of unequal size, one of which, the smaller and more abundantly supplied with protoplasm, becomes the stoma-mother-cell; while the larger, containing less protoplasm, usually forms an ordinary epidermal cell. The stoma-mother-cell becomes elliptical in outline and divides again, by a vertical wall, into the two guard cells, between which, by a splitting of the wall, the intercellular passage (pore) is formed. In cases where the stomatal apparatus has several subsidiary cells either a number of divisions occur in the young epidermal cell before the guard cells arise; or the subsidiary cells are derived from epidermal cells adjoining that which gives rise to the stoma.

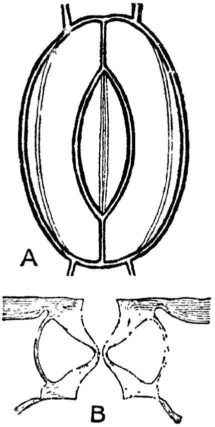

FIG. 45.

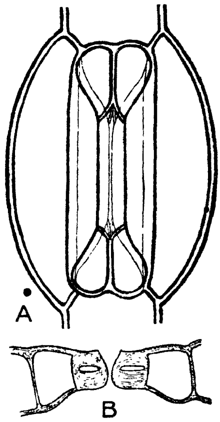

FIG. 46.

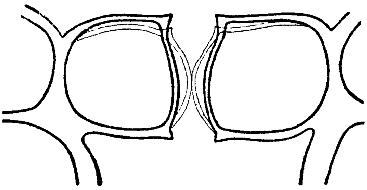

FIG. 47.

FIGS. 45-47.—Types of Stomatal Apparatus. The thick lines indicate the form of the guard cells in the open condition, the thin lines when the stoma is closed.

FIG. 45.—Type of the Amaryllidaceae. *A*, Surface view. *B*, In transverse section.

FIG. 46.—Type of the Gramineae with the two subsidiary cells. *A*, Surface view. *B*, Transverse section.

FIG. 47.—*Mnium*-type in transverse section. (After HABERLANDT.) Further description in the text.

3. HAIRS.—The epidermis of almost all plants bears hairs (trichomes). They are sometimes unicellular structures and form papillate (Fig. 48), tubular (Fig. 151), or pointed (Figs. 49, 50, 53 to the left) protrusions of the epidermal cells. In other cases they are multicellular and form cell-rows, stalked or unstalked cell-surfaces (scale-hairs, Fig. 52) which may resemble small leaves as in the ramenta of Ferns, or cell-masses. The multicellular trichomes are also developed from young epidermal cells, and, indeed, usually proceed from a single initial cell of the hair by its growth and subdivision. Unicellular and multicellular hairs may further be unbranched or branched (Fig. 51, stellate hairs). Their walls may be thin and delicate or strongly thickened and frequently calcified or impregnated with silica, and sharply pointed at the tip (bristles, Fig. 49, right). The protoplasts may remain alive and resemble those of the epidermal cells, or may die. In the latter case the cavity often becomes filled with air and the hair appears white, or it may be

laterally compressed as in the case of the long hairs of the cotton-seed (Fig. 50) from which the cotton of commerce is obtained. The basal portion of the hair in the epidermis may be distinguished from the freely projecting body of the hair. The epidermal cells around the base are often arranged in a ring or radiate on all sides, and may be called the subsidiary cells of the hair. The STINGING HAIRS (Fig. 49), such as those of Nettles (*Urtica*) and of the Loasaceae, are special forms of bristles.

They arise from single epidermal cells which swell in the course of their development, and becoming surrounded by adjoining epidermal cells present the appearance of being set in sockets; at the same time, by the multiplication of the cells in the tissue at their base, the whole hair becomes elevated on a column-like protuberance. The hair tapers towards the apex and terminates, somewhat obliquely, in a small head, just below which the wall of the hair remains unthickened. As the wall of the hair is silicified at the end and calcified for the rest of its length, the whole hair is extremely stiff. The heads break off at the slightest touch, and the hairs piercing the skin pour out their poisonous contents, which, especially in the case of some tropical nettles, may cause severe inflammation (41).

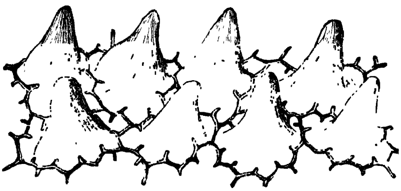

FIG. 48.—Surface of the upper epidermis of a petal of *Viola tricolor*, showing ridge-like infoldings of the lateral walls, and protruding papillae. (× 250. After H. SCHENCK.)

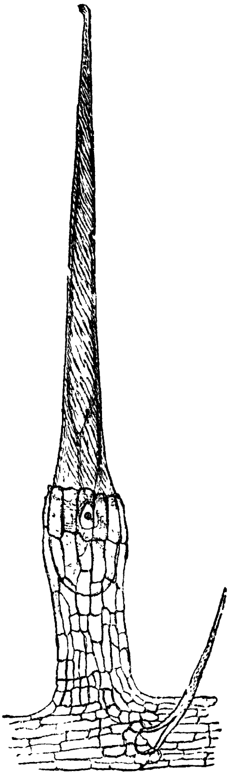

FIG. 49.—Stinging hair of *Urtica dioica*, with a portion of the epidermis, and, to the right, a small bristle. (× 60. After STRASBURGER.)

Hairs have thus various forms and perform very different functions. They frequently contribute to the protection afforded by the epidermis, forming a covering to full-grown parts of the plant and very frequently to the young parts in the bud or expanding from this. Such coverings, which may be composed of dead woolly hairs, serve to diminish the transpiration and are a protection against direct sunlight. Special hairs serve for the absorption of water and other substances (cf. Fig. 151). Very diverse substances are excreted by glandular hairs (Figs. 72-74).

Certain hairs with abundant protoplasm and peculiar structure serve to receive mechanical stimuli according to G. HABERLANDT (42). They occur on stamens, petals, and the joints of leaves, and are known as tactile papillae, hairs, or bristles.

4. EMERGENCES, unlike hairs, are not formed solely by epidermal cells, but a number of cells, lying more or less deeply in the sub-epidermal tissues, also take part in their formation. They are sometimes glandular, and in other cases serve as organs of attachment.

Thus, for example, only a few rows of sub-epidermal cells enter into the formation of the emergences (Fig. 53) on the margins of the stipules of the Pansy (*Viola tricolor*), which are glandular. Deeper-lying tissue takes part in the construction of the anchor-shaped attaching organs, over 1 mm. long, which clothe the fruit of the Hounds-tongue (*Cynoglossum*) and lead to its dispersal by means of animals. The prickles of the Rose or Bramble are still larger emergences that are of assistance in climbing. The tentacles of *Drosera* (Fig. 208) are also emergences.

(b) Boundary Tissue formed of Corky Cells.—When the epidermis does not remain alive and functional during the life of the organ which it covers, the tissues of the body become limited and protected even more efficiently by suberised cells. Such cells also in the form of layers or sheaths serve to bound and delimit certain living masses of tissue from others within the plant body. Their origin may be primary or secondary. The suberisation is brought about by suberised lamellae

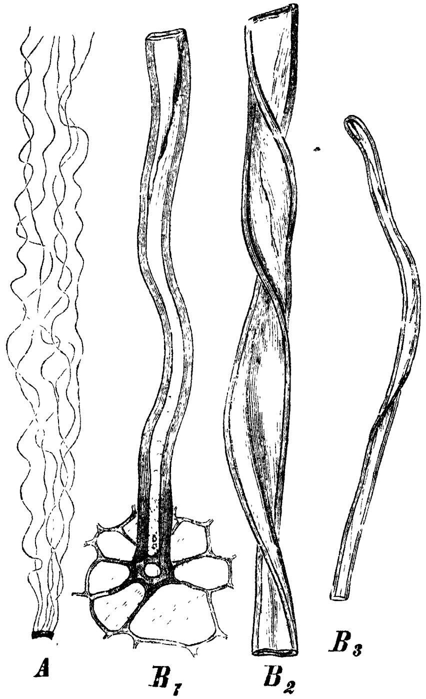

FIG. 50.—Seed-hairs of the Cotton, *Gossypium herbaceum*. *A*, Part of seed-coat with hairs (× 3). B_1, Insertion and lower part, B_2, middle part, and B_3, upper part, of a hair. (× 300. After STRASBURGER.)

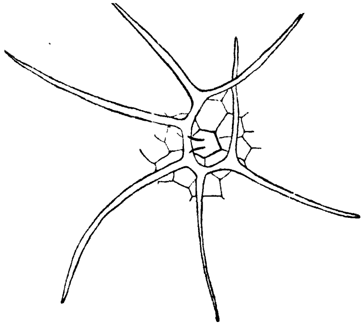

FIG. 51.—Stellate hair in surface view from the lower epidermis of the leaf of *Matthiola annua*. (× 90. After STRASBURGER.)

being deposited on the pre-existing wall forming secondary thickening layers, while succeeding layers of the wall remain unsuberised and frequently become lignified. Three kinds of suberised boundary tissues can be recognised: (1) the cutis tissue; (2) the endodermis; (3) the cork.

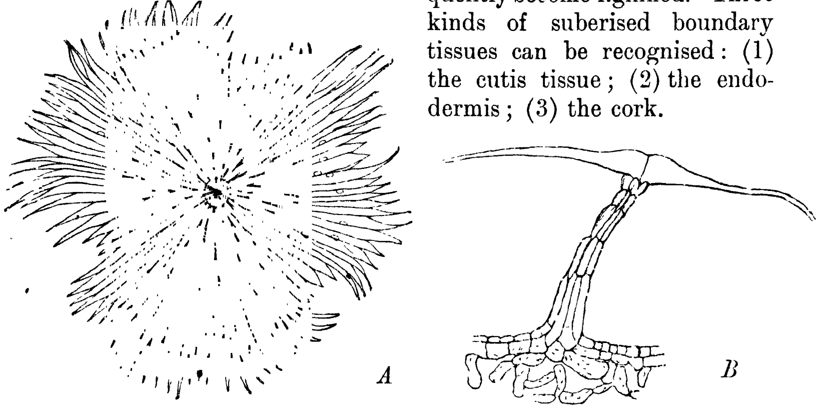

FIG. 52.—Scale-hair from the lower side of the leaf of *Shepherdia canadensis*. *A*, Surface view. *B*, Longitudinal section. (× 240. After STRASBURGER.)

(1) **The Cutis Tissue** is a primary permanent tissue and arises by the early suberisation of cells of the epidermis or of thinner or thicker layers of parenchyma from which intercellular spaces are frequently absent. A tissue of the latter kind not uncommonly sheathes the outside of older parts of the plant (e.g. roots, Fig. 153 *cx*) the epidermis of which has perished earlier. The cells of this cutis tissue usually retain their living contents.

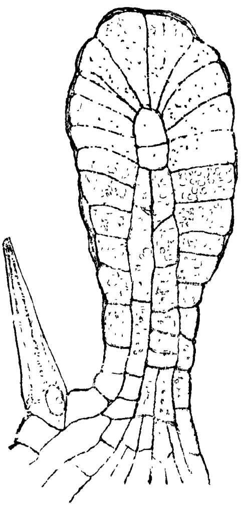

FIG. 53.—Glandular emergence from a stipule of *Viola tricolor*, showing also to the left a unicellular hair. (× 240. After STRASBURGER.)

(2) **Endodermis.** — This tissue is formed of the endodermal cells ([43]). It very frequently encloses and bounds, as a sheath a single layer of cells in thickness, living tissues within the plant. Its origin is usually primary. The elongated prismatic living cells of the endodermis have no intercellular spaces between them. When young the walls are not suberised, but a narrow strip of the membrane, in the form of a band running completely round the cell, has undergone a peculiar change by the introduction of an imperfectly known (? corky or woody) substance (Caspary's band, Fig. 54 *A*). This band gives the appearance of a dark dot or a dark lens-shaped body (Fig. 54 *B*, Fig. 154 *S*) in transverse sections, while it appears as an undulated band in radial longitudinal section. In older endodermal cells, as in the cells of the cutis, a secondary layer of

corky substance is deposited all over the wall, and thick tertiary layers of carbohydrate material that often become strongly lignified may follow on this.

(3) Cork.—While the endodermis and the cutis tissue are always primary permanent tissues the cork is always a secondary tissue, and is developed from a secondary meristem known as the CORK CAMBIUM. The cork forms either a thin peripheral layer a number of cells thick which is smooth and of a grey colour, or thicker, fissured coverings of cork composed of radial rows of cells (Figs. 55, 56). It forms where the epidermis has been thrown off, or where living parenchyma has been exposed by wounds. The cork-cells usually contain air and are brown, owing to the dead cell contents. They have a flattened prismatic form and are extended tangentially (Fig. 56 *A*), fitting together without intercellular spaces. The secondary layers of the wall are suberised, while the middle lamella is often lignified. Tertiary thickening layers are either wanting or consist of cellulose, forming the so-called cellulose layer, which may sometimes become lignified. Even a thin layer of cork a few cells deep (Fig. 56) greatly diminishes the transpiration from the surface of any part of the plant, and, as will readily be understood, much more than the epidermis does. Thicker zones of cork also prevent the entry of parasites. Since cork is a poor conductor of heat it also protects the plant against overheating.

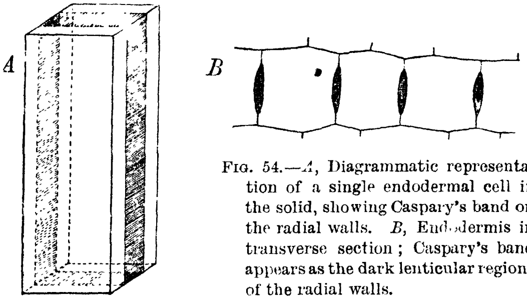

FIG. 54.—*A*, Diagrammatic representation of a single endodermal cell in the solid, showing Caspary's band on the radial walls. *B*, Endodermis in transverse section; Caspary's band appears as the dark lenticular regions of the radial walls.

Many old stems, tubers, bud scales, and fruits are covered with a layer of cork; thus the skin of a potato is of this nature. Bottle-cork is obtained from the Cork Oak. The cork here consists of broad layers of thin-walled, wide cork-cells (Fig. 55) alternating with which are thinner layers of more flattened cork-cells which mark the annual limits of growth; this can be recognised in an ordinary cork. The first layer of cork of the Cork Oak is artificially stripped down to the cork-cambium after fifteen years. A new cambium then forms a few cells deeper, which provides the cork of economic value; this is removed every 6 to 8 years.

The mature cells of cork are very rarely pitted, and either remain relatively thin or are more or less strongly thickened (Figs. 56, 178 *p*). Strongly thickened cork cells form what is known as STONE CORK.

Frequently layers of suberised and unsuberised cells alternate in a corky tissue. The latter cells, which do not differ greatly from the cork-cells in structure and contents and may be thin- or thick-walled, arise in the same way and are called PHELLOID TISSUE.

LENTICELS.—The formation of a covering of cork without intercellular spaces in place of the epidermis would prevent gaseous exchange between the interior of the stem and the atmosphere were the stomata not replaced in some way. This is effected by the development of lenticels, rough porous warts elongated or spindle-shaped in outline, which are readily seen by the naked eye on the cork of most trees. They consist of dead unsuberised tissue rich in intercellular spaces (COMPLEMENTARY TISSUE) interrupting the layer of cork (Fig. 57). The intercellular spaces open on the one hand to the atmosphere, and on the other are in communication with the ventilating system of the underlying living tissues.

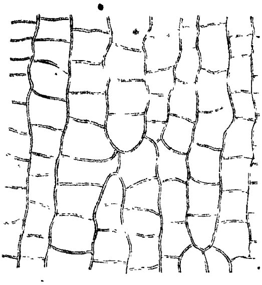

FIG. 55.—Transverse section of bottle-cork. (× 120.)

In bottle-cork the lenticels form the pores, filled with a brown powder derived from the dead cells. These pores run radially through the cork.

The lenticels frequently form beneath stomata and at an early stage in the development of the cork. The cork cambium which appears beneath the stoma has radially-running intercellular spaces between its cells (Fig. 57 *pl*), and forms to the outside complementary cells separated by intercellular spaces (Fig. 57 *l*). The lenticel soon breaks through the epidermis. Alternating with the complementary tissue the cork cambium in the lenticels forms layers of more closely-connected suberised and lignified cells (intermediate bands or closing layers). These are developed to close the lenticel during the winter and are again ruptured in the spring.

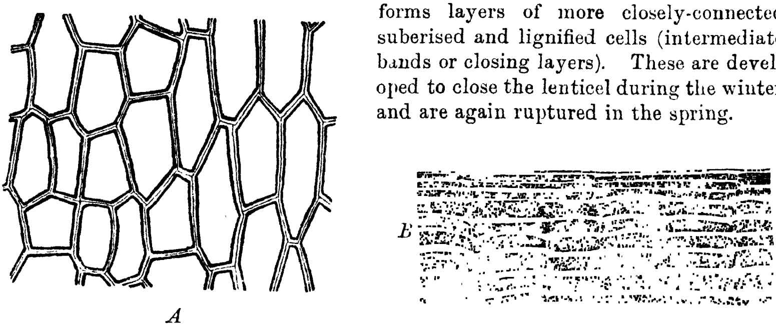

FIG. 56.—*A*, Tangential section; *B*, Transverse section of the cork layer of a Lime twig. The cell-walls in *B* are left white, while the dead contents are dotted. (× 120.)

The BARK, composed of a more complicated set of tissues than the cork, forms a covering on old stems and roots (cf. p. 154).

3. The Mechanical Tissue System (44).—Without a certain amount of rigidity the definite form which is essential to the performance of their functions in most plants would be inconceivable. In isolated cells and in growing tissues this rigidity is attained by turgor (cf. p. 219) and tissue-tensions (cf. p. 277). Since, however, turgor and tissue-tensions are destroyed by any great loss of water, leading to the wilting of the plant, they do not alone confer the necessary rigidity upon plants and in particular, land-plants. How great are the demands made upon the stability of plants will be at once apparent from a consideration of a Rye haulm which has a height of 1500 mm., and is at its base scarcely 3 mm. in diameter. In addition, moreover, to the great disproportion between the height and diameter of plants, they often support a heavy weight at the summit; the Rye straw must sustain the burden of its ear of grain, the slender Palm the heavy and wind-swayed leaves (which in species of *Raphia* have a length of 15 m. and a corresponding breadth), while at times the weight of the bunches of fruit has also to be considered. In plants, however, the rigid immobility of a building is not required, and they possess instead a wonderful degree of ELASTICITY. The Rye straw bends before the wind, but only to return to its original position when the force of the wind has been expended. The mechanical equipment of plants is peculiar to themselves, but perfectly adapted to their needs. The firm but at the same time elastic material which plants produce is put to the most varied uses by mankind; the wood forms an easily worked yet sufficiently durable building material, and the bast fibres are used in the manufacture of thread and cordage and textile fabrics (*e.g.* linen).

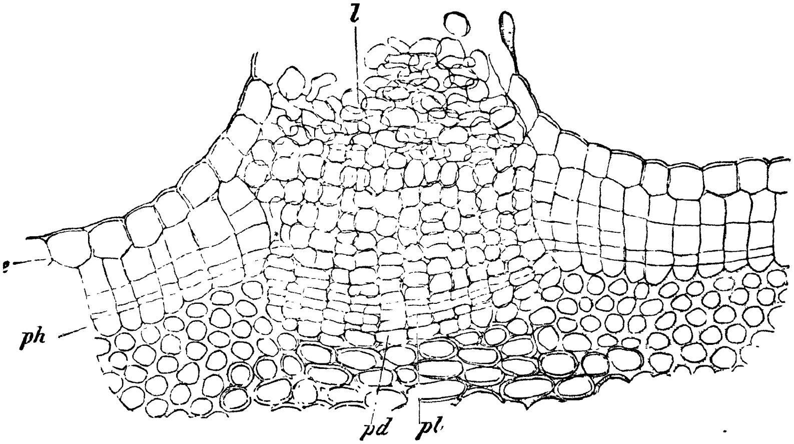

FIG. 57.—Transverse section of a lenticel of *Sambucus nigra*. *e*, Epidermis; *ph*, phellogen; *l*, complementary cells; *pl*, phellogen of the lenticel; *pd*, phelloderm. (× 90. After STRASBURGER.)

This type of stability depends on special tissues, known as the STEREOME, composed of cells with strongly thickened walls. These tissues are the SCLERENCHYMA and COLLENCHYMA.

(a) Sclerenchyma.—This is the typical mechanical tissue of fully-grown parts of the plant and is formed of SCLERENCHYMA CELLS (stone cells) or SCLERENCHYMA FIBRES (bast fibres). Both when mature are as a rule dead cells with strongly thickened walls consisting of lamellae of carbohydrate material, which is often lignified. The sclerenchymatous cells or stone cells (Fig. 29) are more or less isodiametric and polyhedral and have round, branched, or unbranched pits. The sclerenchymatous fibres (Fig. 58), on the other hand, are narrow, elongated, spindle-shaped cells with pointed ends, polygonal in transverse section (Fig. 59). They have obliquely-placed, narrow, elliptical pits. Their cell-walls may be almost completely unlignified (*e.g.* flax) or more or less lignified (*e.g.* hemp). In their development sliding growth frequently occurs and they only mature in fully-grown parts of the plant. Sclerenchymatous fibres have always a length which for a plant cell is considerable, on the average 1-2 mm. In some plants they are much longer, *e.g.* 20-40 mm. in Flax, to 77 mm. in the Stinging Nettle, and in *Boehmeria* even 220 mm. Such long fibres are of economic importance in the manufacture of textile fabrics.

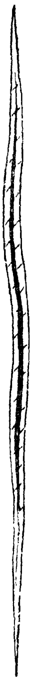

FIG. 58.—A sclerenchymatous fibre. (× about 100. After STRASBURGER.)

Sclerenchymatous cells and fibres may occur singly as in some leaves, when they may also be branched. Usually, especially in the case of the fibres, they are closely associated in strands, bands, rings, or sheaths, variously arranged so as to ensure the requisite rigidity of the organ against bending, tension, or pressure while employing the least mechanical tissue. Rigidity against compression as it is met with in the shells of nuts and the stones of some fruits is usually dependent on a tissue composed of stone-cells. The rigidity of stems and roots against bending and pulling is due to sclerenchyma fibres. Both types of mechanical tissue render the organs in which they occur resistant to cutting or other mechanical injury.

The firmness of the individual cells depends on the thickening of their cell-walls. The resistance to tearing offered by the strands of sclerenchymatous tissue is due on the other hand to the interlocking of the elongated fibres.

According to SCHWENDENER'S investigations, the sustaining strength of sclerenchymatous fibres is, within the limits of their elasticity, in general equal to the best wrought iron or hammered steel, while at the same time their extensibility is ten or fifteen times as great as that of wrought-iron. It is true that soon after exceeding its limit of elasticity the stereome of the plant becomes ruptured, while the limit of rigidity for iron is not reached until the load is increased threefold.

(**b**) **Collenchyma.**—The elements of the sclerenchyma are no longer in a condition which allows of growth, and it cannot be employed in parts of the plant which are still actively elongating. Where such parts of the plant require special strengthening in addition to that given by the tensions of cells and tissues, this is obtained by means of COLLENCHYMA, which is a living tissue, capable of growth

The collenchymatous cells may be isodiametric but are usually elongated ; they have transverse end walls (Fig. 61) or are pointed. They resemble the cells of the parenchyma, and, like them, often contain chloroplasts, but differ in the unequal thickening of their cellulose walls. This is localised at the angles (angle collenchyma, Fig. 60) or on the tangential walls (surface collenchyma). Intercellular spaces are absent or are very small. Collenchyma possesses a considerable rigidity against tearing owing to the thickening of the walls of its component elements. The extensive unthickened regions of the cell-walls enable materials to be rapidly transported within this tissue. The distribution of collenchyma in the plant corresponds to its particular mechanical properties.

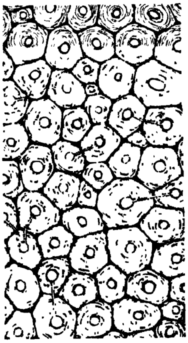

FIG. 59.—Transverse section of the sclerenchyma in the leaf of *Phormium tenax*. (× 240.)

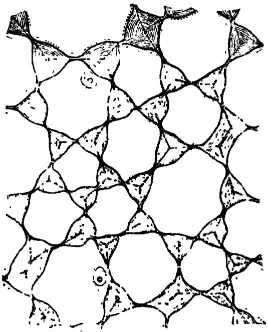

FIG. 60.—Transverse section of the collenchyma of *Cucurbita Pepo*. (× 240.)

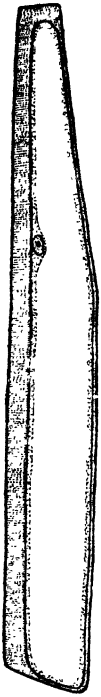

FIG. 61.—A collenchymatous cell seen from the side. (× 240.)

4. The Conducting Tissues.—As the body of a plant becomes larger and composed of more numerous cells, and especially as more parts of it project from the soil or water into the air, the need of rapid conduction of substances, from one organ to another (*e.g.* from leaves to roots and conversely) increases. The movement of diffusion through the cross walls even of elongated parenchymatous cells does not suffice, though facilitated by the presence of pits in the wall. Special conducting tissues have therefore arisen, the characteristically constructed elements of which are usually elongated in the main direction of conduction, frequently present enlarged surfaces for diffusion, and are further as a rule united to form continuous conducting channels. Such tissues are always associated in a connected system traversing the whole plant. The absence of intercellular spaces is further characteristic of them.

(a) Sieve-Tubes.—The living elements composing the SIEVE-TUBES (^{45}) are arranged in longitudinal rows and connected by open pores which appear to serve for the transport of organic substances. The transverse or oblique ends, and sometimes the lateral walls, have sieve-like perforated regions the pores of which are filled with protoplasmic strands. These are called the SIEVE-PLATES (Fig. 62 *A*, *B*).

In many plants (*e.g.* the Cucumber, Fig. 62 *A*) the entire transverse wall forms one sieve-plate perforated by relatively coarse pores. On the longitudinal walls the sieve-plates have the form of narrowly circumscribed, circular areas with much finer pores (Fig. 62 *C*, *c**) where two sieve-tubes adjoin laterally. In other cases several finely-perforated areas (sieve-plates) are found on the oblique end-wall of a sieve-tube (Fig. 63).

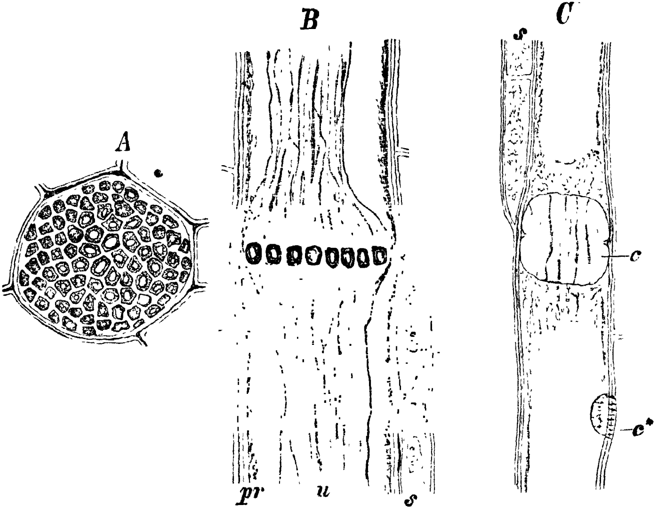

FIG. 62.—Parts of sieve-tubes of *Cucurbita Pepo*, hardened in alcohol. *A*, Surface view of a sieve-plate. *B*, *C*, Longitudinal sections, showing segments of sieve-tubes. *s*, Companion cells; *u*, mucilaginous contents; *pr*, peripheral cytoplasm; *c*, callus plate; *c**, small, lateral sieve-plate with callus. (× 540. After STRASBURGER.)

The elements of a sieve-tube, each of which corresponds to a cell, contain a thin living protoplasmic layer lining the wall, with a single nucleus, leucoplasts, and often starch-grains. This encloses a watery, alkaline, more or less concentrated and coagulable cell-sap which is rich in albuminous substances and frequently in carbohydrates and inorganic salts (phosphates) (Fig. 62 *Bu*). The walls of sieve-tubes are almost always unlignified; they consist of cellulose and are elastically stretched by their contents. As a rule sieve-tubes remain functional during one vegetative period only. Before passing into the inactive condition their sieve-plates become covered by highly refractive plates of CALLUS (Fig. 62 *C*), which diminishes or prevents the exchange of materials between the members of the sieve-tube. If the sieve-tube resumes its function in the succeeding vegetative period this callus is again dissolved.

The callus plates consist of CALLOSE, a substance the chemical composition of which is still unknown; this is characterised by its insolubility in ammonia-oxide of copper and its solubility in cold 1 % solution of potash. It is coloured reddish-brown by chlor-zinc-iodide, a shining blue with aniline blue, and shining red with corallin (rosolic acid). The portions of the wall bounding the pores of a sieve-plate are coated with a thin layer of callose while the pores are still open. It is by the gradual thickening of this layer that the pores become narrowed and ultimately occluded.

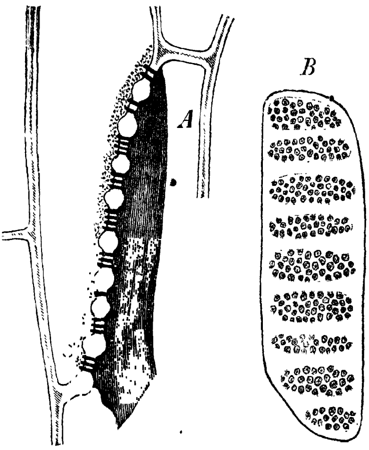

FIG. 63.—*A*, Junction of two elements of a sieve-tube of *Vitis vinifera*, the oblique wall being shown in section. (× 600. After DE BARY.) *B*, A similar wall in surface view showing the sieve-pits. (Diagrammatised by ROTHERT after DE BARY.)

(b) Vessels.—Special, and ultimately dead, cells, which are tube-like with a circular or polygonal cross-section and are elongated and arranged in longitudinal rows, serve for the conduction and sometimes also for the storage of water in the plant. The lignified walls of these vessels have striking and characteristic thickening. So long as they are functional the vessels contain water. They are distinguished as TRACHEIDES and TRACHEAE. The tracheides are single cells with pointed ends, and are as a rule of narrow diameter. Their walls bear peculiar pits (Fig. 67 *B*). These elements frequently also serve as mechanical tissue, as in the stems of Coniferae. The tracheae, on the other hand, are wider or narrower tubes formed from a number of cells by the disappearance of their end-walls.

When the end-walls are transversely placed they are completely dissolved, leaving only a narrow annular rim which becomes further thickened (Figs. 64 *C*, *s*, 66 *I*. *q*, *q'*). Obliquely placed end-walls, on the other hand, are usually not pierced by a single large opening but by a number of elliptical openings placed one above the other (scalariform perforation, Figs. 66 *II*., 166 *tg*). Some of the end-walls are not perforated but merely pitted, and the vessels are thus of limited length.

Some tracheae, in particular those of woody climbers or lianes, may be some metres in length. In the Oak also tracheae two metres in length are frequent. As a rule, however, they do not exceed 1 m. and are usually only about 10 cm. in length. The widest as well as the longest vessels are met with in climbing plants; in them they may be 0·7 mm. wide, while those of the Oak are about 0·25 mm. and of the Lime 0·06 mm.

As a rule, in botanical literature, a distinction is drawn between tracheides and tracheae or vessels. DE BARY, however, called all these elements tracheae and distinguished between tracheides and vessels. The most convenient course, which is adopted here, is to distinguish within the collective conception vessels the tracheides and tracheae.

The thickening of the walls of vessels may have the form of narrow bars (Fig. 64, 65), on the relatively thin wall. These bars may form isolated rings, connected spirals, or a network, and accordingly ANNULAR, SPIRAL, and RETICULATE tracheides and tracheae are distinguished (Figs. 64, 65). In other cases the thickening involves the greater part of the cell-wall but leaves numerous pits (PITTED VESSELS, Figs. 66, 67). The pits may be circular, polygonal, or more or less transversely extended and elliptical or slit-like. When transversely-extended pits stand above one another in regular rows on the lateral walls the vessel is termed SCALARIFORM (Fig. 66 *II.*, 67 *A*). Transition forms are met with between the various types of vessels.

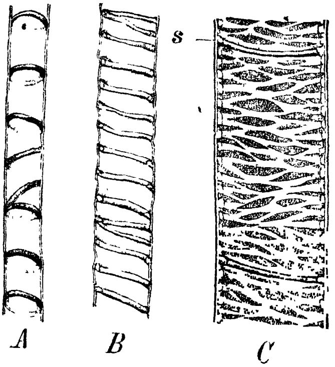

FIG. 64.—*A*, Part of an annular tracheide. *B*, Part of a spiral tracheide. *C*, Longitudinal section through part of a reticulate trachea showing the remains of a partition wall, *s*. (× 240. After H. SCHENCK.)

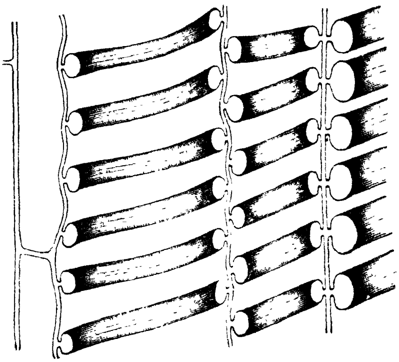

FIG. 65.—Portion of a longitudinal section through three spiral vessels and a row of parenchyma cells of the Gourd (*Cucurbita Pepo*). (× 560. After W. ROTHERT.)

Only the annular or spiral vessels can undergo extension or stretching. On this account they are the only kinds present in growing parts of plants.

The pits of pitted vessels are always BORDERED PITS, the canal of which widens from the cell-lumen to the pit-membrane (Fig. 68 *C*). They may be present on one or both sides of a cell-wall. The outline of the pit in surface view is commonly circular and encloses a smaller circle (Fig. 68 *A*). The smaller circle is the opening into the cell-cavity, while the wider outline is that of the pit-cavity at its widest part adjoining the pit-membrane. The thickening of the cell-wall thus overhangs the pit-membrane and forms the wall of the pit, between the outer and inner circles. The pit-membrane is frequently thickened in the centre, forming the TORUS (Fig. 68 *C*), and this, when the membrane is deflected to one or other side, may close the entrance like a valve (Fig. 68 *B*, *t*). The wide membrane of the bordered pits allows readily of movements of water from the one cell-cavity to the other, while the overhanging wall of the pit ensures that the rigidity of the wall is not unduly diminished. As Fig. 68 *C* shows, the pits are bordered on both sides of a wall separating two water-conducting elements. When, however, a vessel abuts on a living cell, the pit is only bordered on the side of the membrane toward the water-conducting element and the pit-membrane has no torus. On the other side of the wall a simple pit is developed.

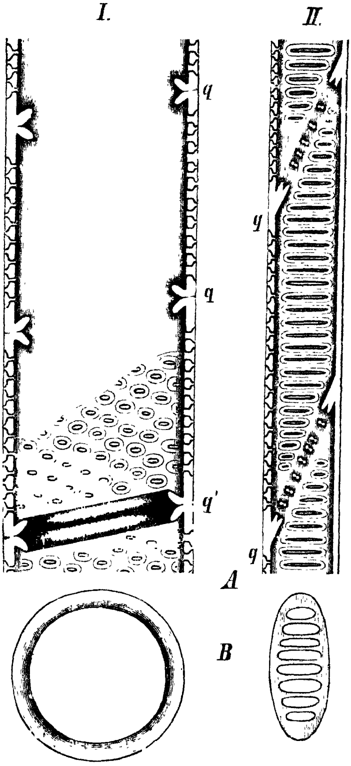

FIG. 66.—*A*, Diagrams of tracheae in longitudinal section. *I.*, Wide trachea with small elliptical bordered pits, and with simple perforation of the end-wall (*q*, *q*). The further portion of the wall is cut away in the upper portion of the figure. *II.*, Narrow trachea with scalariform pitting of the wall and perforation of the transverse wall, *q*. *B*, The transverse walls of the two tracheae in surface view. (After ROTHERT.)

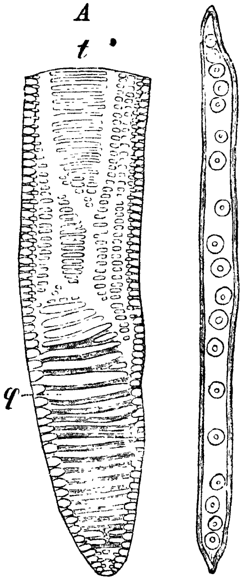

FIG. 67.—*A*, Lower third of a scalariform tracheide from the rhizome of the Bracken Fern (*Pteridium aquilinum*); *t*, the lateral walls; *q*, the end-wall. (× 95. After DE BARY.) *B*, A tracheide with circular bordered pits. (× 100. After STRASBURGER.)

The pits in the end walls of tracheae and tracheides are also always bordered pits. In the case of the tracheae it is their pit-membranes that are absorbed (cf. Fig. 66 *A I.* and *II.*).

The thickening bands in annular and spiral vessels correspond to the walls of the bordered pits (46). These thickening bars are in fact always narrowed at their attachment to the wall of the vessel (Fig. 65).

On this account the spiral thickening bands are readily detached from the walls in the preparation of sections, and appear as if lying within the cavity of the vessel. The thin portions of the wall between the thickenings correspond to the pit-membranes, and, when occurring between two water-conducting elements, may be somewhat thickened like a torus.

The thickening of the walls of water-conducting elements increases the mechanical rigidity of the latter and prevents their being crushed by the adjoining living cells. The living contents of the vessels diminish as the wall thickens and ultimately completely disappear. This does not happen in the tracheae until after the transverse walls have been broken through.

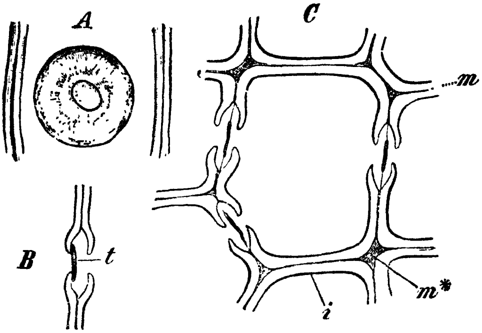

FIG. 68.—Tracheides from the wood of the Pine, *Pinus sylvestris*. *A*, Bordered pit in surface view. *B*, Transverse section of bordered pit from a tangential section of the wood; *t*, torus. *C*, Transverse section of a tracheide; *m*, middle lamella, with gusset, *m**; *i*, thickening layers of the wall. (× 540. After STRASBURGER.)

System of Tissue of the Vascular Bundles.—The sieve-tubes are usually associated with conducting parenchyma to form strands or bundles of phloem which traverse the plant. The same holds for the tracheides and tracheae, although isolated or grouped tracheides may occur as a water-storage tissue in the parenchyma.

Such strands of phloem or of vascular tissue may be regarded as INCOMPLETE VASCULAR BUNDLES. They are common in the secondary permanent tissue as vascular strands in the wood and phloem strands in the bast (cf. pp. 140, 149). In the primary tissues, however, the phloem and vascular strands are united to form COMPLETE VASCULAR BUNDLES which run as a rule parallel to the long axis of an organ, and are united by cross connections into a network. The name VASCULAR BUNDLE SYSTEM is given to this striking feature in the construction of a plant. In these bundles the elements which serve for the conduction of water are associated with those which conduct organic material, so that these different substances follow nearly the same course, though usually in opposite directions. Such complete vascular bundles contrast with the less dense surrounding tissue by the narrowness of their elements, and the absence of intercellular spaces; they are often visible to the naked eye as in the translucent stems of *Impatiens parviflora.*

The complete conducting bundles are also termed vascular bundles, fibro-vascular bundles, or mestome.

5. Secretory Cells and Secretory Tissue. (1) SOLITARY CELLS.—Secretory cells isolated or arranged in rows are of frequent occurrence in the most diverse tissues. They may be isodiametric or tubular, and contrast with the other cells by reason mainly of their contents. Within their diminished or dead protoplasts secretions of the most varied kinds are contained. These are end-products of the metabolism and may have an ecological significance as protective substances. Mucilage, gums, ethereal oils, resin, gum-resin, tannin, alkaloids, and crystals of oxalic acid (Fig. 21) are among the most frequent secretions. The walls of these cells are often suberised.

The non-septate LATICIFEROUS CELLS which contain the secretion called LATEX belong here. They are richly-branched tubes without cross-walls, with a smooth elastic cellulose wall that is usually unthickened (Fig. 69). They have a layer of living protoplasm with numerous nuclei lining the wall and sometimes contain starch-grains ([47]), which in many Euphorbiaceae are dumb-bell-shaped. Their cell-sap is a milky, usually white, watery fluid which rapidly coagulates on exposure to the air. The latex serves to close wounds and as a protection against vegetable-feeding animals. The laticiferous cells have on the other hand no conducting functions.

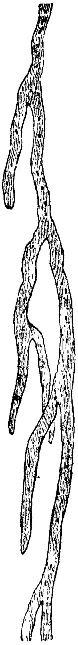
FIG. 69.—Portion of a laticiferous cell of *Ceropegia.* (× 150. After STRASBURGER.)

The laticiferous tubes in many Euphorbiaceae (*e.g. Euphorbia*), Moraceae, Apocynaceae, and Asclepiadaceae proceed from cells which are already recognisable in the embryonic plant, and with the growth of the latter continue to grow, branch, and penetrate all the organs so that they may become many metres in length.

Tannins, glucosides, poisonous alkaloids, and especially calcium-malate, occur dissolved in the latex; peptonising enzymes in *Ficus Carica* and *Carica Papaya*; further, as droplets in an emulsion, gum-resins (mixtures of gum and resin), caoutchouc ($C_{25}H_{40}$), gutta-percha, fats, and wax occur, and as a solid constituent proteid granules.

(2) CELL-FUSIONS.—A number of secretory cells may unite to form

a more spacious reservoir for the secretion, by the dissolution of the walls between them. This is most strikingly seen in the LATICIFEROUS VESSELS. They resemble the laticiferous cells in appearance and in their contents, but differ in their origin by the fusion of a number of cells forming a network (Fig. 70). Remains of the transverse walls may be recognised in this.

The laticiferous vessels, like the laticiferous cells, are limited to certain families of plants, for instance the Papaveraceae (*Papaver*, *Chelidonium*, with reddish-orange latex), the Campanulaceae, in the Compositae the Cichorieae (*Cichorium*, *Taraxacum*, *Lactuca*, *Scorzonera*, *Hieracium*, *Tragopogon*), and some Euphorbiaceae (*e.g.* the important Rubber tree, *Hevea*).

The MUCILAGE TUBES which occur in many Monocotyledons are in many respects similar to the laticiferous vessels. Their mucilaginous sap consists of albumen, starch, glucose, tannins, and inorganic substances.

(3) LYSIGENOUS INTERCELLULAR SPACES.—Secretory reservoirs frequently arise as spherical, irregular, or tubular cavities by dissolution of entire secretory cells, *i.e.* lysigenously (Fig. 71). These lysigenous secretory reservoirs arise from groups of cells in which the secretion has been formed and the walls gradually dissolved. The secretory cavities filled with ethereal oils in the orange and lemon, other Rutaceae, and many Myrtaceae have this origin.

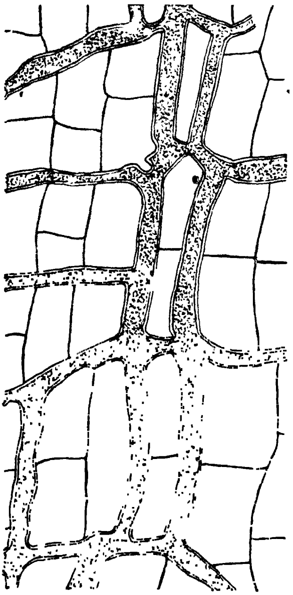

FIG. 70.—Tangential section through the periphery of the root of the Dandelion (*Taraxacum*) showing reticulately united laticiferous vessels. (× 240.)

6. Glandular Cells and Glandular Tissue.—Glandular cells, which excrete substances from their protoplasts to the outside or into the intercellular spaces, occur singly or in groups in the epidermis, in the parenchyma, and in other tissues. The glandular cells resemble parenchymatous cells, but have as a rule abundant protoplasm and large nuclei as in meristematic cells. The excreted substances frequently have an ecological significance. Closely connected glandular cells forming a layer constitute a GLANDULAR EPITHELIUM.

Glandular epithelia or isolated glandular cells are of frequent occurrence in the epidermis and are often covered by a porous cuticle or a cuticle may be wanting. In this situation glandular hairs, the knob-shaped terminal cell of which is secretory (capitate hairs, Fig. 72), also occur. Other glandular hairs may be scale-shaped (Fig. 73), and glandular emergences (Fig. 53) are also found. The secretion is very often composed of resinous substances, and accumulates between the outer wall of the secretory cells and the cuticle, which is raised up and finally burst. The same holds for the formation of other adhesive substances and mucilage.

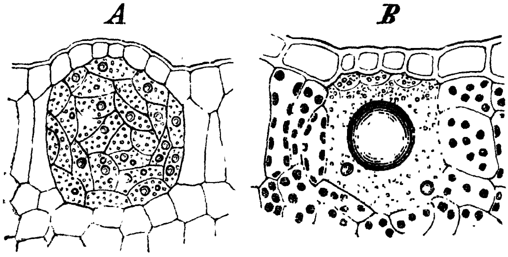

Fig. 71.—Lysigenous oil-reservoirs from the leaf of *Dictamnu fraxinella*. *A*, Young. *B*, Mature after dissolution of the cell-walls. (Rothert altered from Rauter.)

According to the excreted products, which may have varied ecological uses, the epidermal glands may be distinguished into mucilage, oil, resin, digestive (Fig. 74) glands, also salt glands, water glands (hydathodes), and nectaries ([48]). The last-named secrete a sugary fluid which attracts insects and occur as glandular surfaces or hairs within the flower or in other situations (cf. Fig. 136 *n*). These are termed respectively floral and extrafloral nectaries (cf. also p. 109).

The glandular cells or epithelia, enclosed within parenchymatous or other tissues, always abut on circular or irregular intercellular spaces or tubular, branched, or unbranched canals, which sometimes run through the whole plant as a connected system of tubes. These intercellular spaces, which arise by the splitting apart of cells, form the SCHIZOGENOUS SECRETORY RESERVOIRS (Fig. 75). Their contents consist of ethereal oils, resin, gum, or mucilage, and corresponding distinctions are made in naming these canals. Resin-canals are met with in many Coniferae,

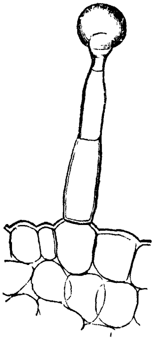

Fig. 72.—Glandular hair from the petiole of *Primula sinensis* showing the secretion above. (× 142. After De Bary.)

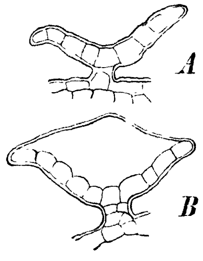

Fig. 73.—Glandular scale from the female inflorescence of the Hop, *Humulus lupulus*, in vertical section. *A*, before. *B*, after the cuticle has become distended by the secretion. In *B* the secretion has been removed by alcohol. (× 142. After De Bary.)

oil-ducts in the Umbelliferae, mucilage- and gum-canals in the Cycadaceae and Araliaceae (*e.g.* the Ivy), and spherical or elongated schizogenous cavities containing ethereal oils in species of *Hypericum* (Fig. 75).

Schizolysigenous reservoirs also occur.

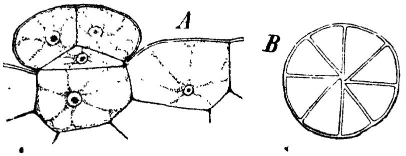

FIG. 74.—Sessile digestive gland from the upper side of the leaf of *Pinguicula vulgaris*. *A*, In longitudinal section. *B*, Seen from above. (ROTHERT altered from FENNER.)

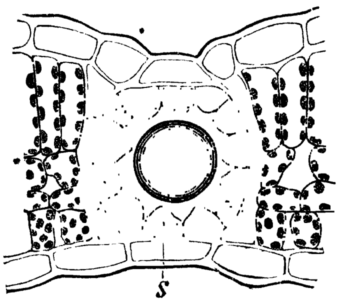

FIG. 75.—Schizogenous oil-reservoir in a cross-section of the leaf of *Hypericum perforatum*. *S*, the glandular epithelium. (After HABERLANDT.)

SECTION III

ORGANOGRAPHY (49)

THE organisms included in the vegetable kingdom are variously shaped and segmented. Some are unicellular throughout life, while others are multicellular. Both may have very simple and regular or irregular outlines and have no external segmentation, or on the other hand may possess a body which is more or less symmetrically segmented and exhibits branching of various kinds.

I. Relations of Symmetry (50).—The form of the whole segmented or unsegmented organism and of its parts is determined by their relations of symmetry. Like nearly all properties of organic forms this is closely connected with the mode of life of the organism and the functions of its organs, especially with the direction of growth of the plant and of its members. As a rule, therefore, the symmetry of the internal construction of a plant corresponds to that of its external form.

Apart from a few very simple forms, the plant-body and its individual parts nearly always exhibit POLARITY and a distinction of base and apex at opposite ends of its longitudinal axis. Such a distinction is shown both in free motile forms, in which the direction of progression is usually determined by the polar construction of the body, and in attached forms, where the organism is attached to the substratum by its basal pole.

Every section through a part of a plant parallel to the longitudinal axis is a longitudinal section. When it passes through the axis it is termed a radial longitudinal section, and when it is at right angles to a radius but not in the plane of the axis itself a tangential longitudinal section. Sections at right angles to the longitudinal axis are transverse sections. An organism or a part of a plant which is almost similarly constructed around its longitudinal axis is termed RADIAL or ACTINOMORPHIC (Fig. 551 *A*). Such a structure can be divided by a number of radial longitudinal sections into approximately equal halves, which are mirror images of one another; it has thus a number of PLANES OF SYMMETRY. When there are only two planes of symmetry standing at right angles to each other the structure is called BILATERAL or bisymmetrical (Fig. 103). Lastly, when there is only a single plane of symmetry (the MEDIAN PLANE) the structure is DORSIVENTRAL or ZYGOMORPHIC; the two lateral halves correspond, while the anterior and dorsal sides are unlike (Fig. 551 *B*). Plants or parts of plants which grow vertically upwards or downwards (ORTHOTROPOUS) are usually radial or bilaterally symmetrical. When, on the other hand, they grow obliquely or at right angles to the vertical (PLAGIOTROPOUS) they are frequently dorsiventral. There are also ASYMMETRICAL organic structures, which cannot be divided by any plane into corresponding halves. Some dorsiventral structures, *e.g.* leaves, become asymmetrical by the one half being differently formed to the other. This is, for example, the case with the leaves of Begonia, and in a less degree with those of the Elm.

The relations of symmetry are of great importance in understanding the general morphological relations of the plant. In many cases the special relations of symmetry of lateral members become intelligible in the light of the symmetry of the whole plant. For example, the asymmetrical leaves of *Begonia* in the light of the dorsiventral symmetry of the more or less plagiotropous plant, or the leaves of Elm and many other plants in the light of their branches.

II. Significance of the External Segmentation to the Organism.—The construction and segmentation of any particular organism stand as a rule in close relation to its needs and mode of life. The external as well as the internal segmentation is usually the expression of a DIVISION OF LABOUR between the parts of a cell or of a multicellular body. The external members are, in fact, usually ORGANS with definite vital functions. The phylogenetic progression from simpler to more segmented organic forms consists in great part in the increase of this differentiation and division of labour.

III. Main Groups of Organs.—The activity of every organism takes place in two directions. It must nourish itself in order to maintain itself as an individual, and it must reproduce in order that the race should not perish with its death. The body of the plant subserves these two fundamental vital impulses. Only in primitive plants does the whole mass serve both equally; usually certain parts are concerned with the nutritive processes and others with reproduction. There is thus usually a clear division of labour between the VEGETATIVE ORGANS and the REPRODUCTIVE ORGANS, which are fundamentally different in form and structure as well as in function. These two groups of organs will require separate consideration.

I. Vegetative Organs

The highest segmentation attained by the vegetative organs of plants is that into ROOT, STEM, and LEAVES. Stem and leaves are classed together as the SHOOT. A plant-body composed of shoot and root is termed a CORMUS, and plants so constructed CORMOPHYTES. The fern-like plants, or Pteridophyta, and the more highly-segmented Seed-plants derived from them are cormophytes.

The cormophytes arose phylogenetically from more simply organised plants in which the plant-body had not attained such a profound segmentation; in which roots were wanting, while leaf-like branches though not true leaves were present. Such structures, as well as quite simple and unsegmented plant-bodies, are included under the term THALLUS, and such plants may be contrasted with the cormophytes as thalloid. The Algae, Fungi, Lichens, and all Bryophyta have thalli.

The thalloid plants must not be confused with the Thallophyta. All thalloid plants possess a thallus, but they are not all Thallophyta. Under this name systematic botany includes only the Algae, Fungi, and Lichens.

A. THE THALLUS (51)

(a) Algae, Fungi. 1. Simplest Forms.—The only forms that are quite unsegmented externally are a number of microscopically small unicellular or multicellular plants. The simplest form that can be assumed by an organism is that of the SPHERE. For example, such spherical cells are shown by some Algae that form a green coating on damp walls (Fig. 34), and by many Bacteria (Fig. 77 *b*). The latter include by far the smallest known organisms.

2. Relative Increase of Surface. Establishment of a Longitudinal Axis.—It is a proposition applicable to all bodies that the smaller they are the greater is their surface relatively to their volume. In the minute cells of Bacteria the surface is thus especially large in relation to the volume, a feature that has an adaptive value in connection with their mode of life.

Of all geometric figures the sphere has the smallest surface for the same volume. All deviations from the spherical form are therefore connected with a relative increase of the surface. In particular, as the volume of the body increases, involving a relative diminution of the surface, the surface-area is in this way increased. Cylindrical, rod-shaped, filamentous, ribbon-shaped, and discoid forms thus occur, and ultimately bodies segmented by reason of their external projections; such bodies usually show a definite LONGITUDINAL AXIS. The free surface of the body is of great importance to the plant for the absorption of the gaseous and liquid substances necessary for its nutrition and derived from the environment. The INCREASE OF SURFACE is thus the most important principle determining the external form of plants.

The unicellular individuals of the beer Yeast (cf. Fig. 19) are ellipsoidal in shape, while the cells of many Algae, such as species of Diatoms (Fig. 76), are discoid or cylindrical. This group of Algae exhibits spindle, canoe, helmet, and fan shapes, and also filamentous ribbon- and chain-like forms. Rod-shaped and spirally-wound forms are met with in the Bacteria (Fig. 77 *a*, *c*, *d*).

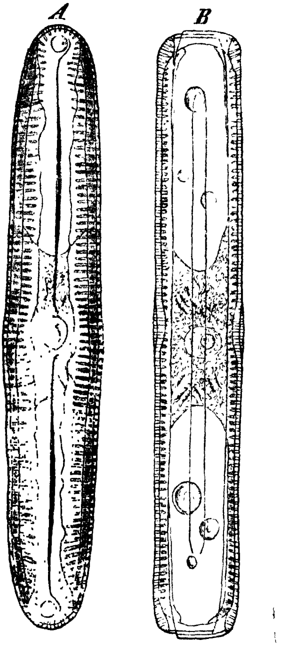

FIG. 76.—*Pinnularia viridis.* *A*, Surface (valve) view. *B*, Lateral (girdle) view. (× 540. After STRASBURGER.)

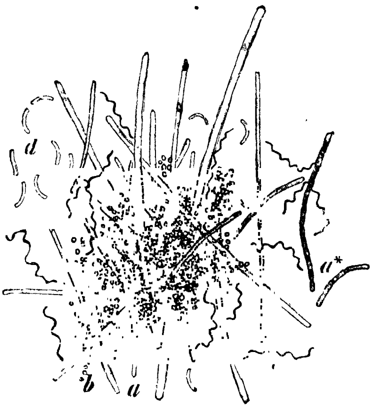

FIG. 77.—Bacteria from deposits on teeth. *a*, *Leptothrix buccalis*; *a**, the same after treatment with iodine; *b*, *Micrococcus*; *c*, *Spirochaete dentium* after treatment with iodine; *d*, *Spirillum sputigenum*. (× 800. After STRASBURGER.)

Such living beings may be attached by mucilage to a substratum or may float free in water. The free-floating organisms of continental water-surfaces as well as of the ocean are termed PLANKTON in contrast to the firmly-attached aquatic organisms which constitute the BENTHOS. Many forms of the plankton flora have the power of active movement (swimming forms) due as a rule to projections of the protoplast as slender contractile flagella or cilia which are special organs of locomotion (cf. Figs. 308, 310-312). This power of movement enables many organisms of the plankton, responding to stimuli, to seek for favourable nutritive conditions or to avoid unfavourable spots. Other forms of the plankton are suspended without true power of movement in the water (floating forms). Many of them, and other plankton organisms, show special arrangements for flotation in the increase of body-surface by long bristles, bars, and plates (Figs. 314, 323, 325). The friction of the body against the water is thus considerably increased and sinking made more difficult (^{52}).

While all these simply organised plants have a fixed outline to their bodies, there are also lower plants which can continually change their form, *e.g.*, the myxomochae and plasmodia of the Myxomycetes.

3. **Establishment of Polarity.**—The next stage in progressive complexity of form is the establishment of the distinction between base and apex. In freely motile forms the cilia are frequently attached at one pole. In fixed forms one pole forms an ORGAN OF ATTACHMENT, as, for instance, a circular disc of attachment or palmately-branched lobes. The further growth may at the same time be restricted to a small region of the body or GROWING POINT. This in intercalary growth is a zone between the base and apex, while in apical growth it is situated at the summit of the plant-body. A young plant of the green seaweed *Ulva lactuca* affords an example of the latter condition (Fig. 78).

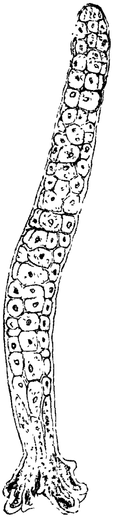

FIG. 78.—*Ulva lactuca*, young stage, showing apex and base. (× 220. After STRASBURGER.)

4. **Flattening.**—Many Algae and Lichens have a disc-shaped or ribbon-shaped thallus (Fig. 80) by which the free surface is further increased. The assumption of this form may therefore be regarded as an adaptation to the nutritive relations of the organism. The latter constructs its organic substance from the carbon dioxide which it can decompose, but this process of assimilation only takes place in plants that contain chlorophyll and in the light. Thus as many chlorophyll grains as possible require to be exposed to the light, and this is attained even in massive bodies by the flattened form.

5. **Dorsiventrality.**—The majority of the forms so far referred to are radial or bilaterally symmetrical. In those in which the thallus spreads out on a substratum (*e.g.* in many Lichens), the construction of the plant body further becomes dorsiventral. Dorsiventral symmetry is characteristic of forms in which the upper side is the more strongly illuminated and is especially concerned in assimilation.

6. **Branching.** — Filamentous, ribbon-shaped, and discoid forms, the surface of which is extended as branches, are still more highly organised. This occurs in most thalli of Algae, Fungi, and Bryophyta. The free surface is still further increased by the branching, and the available space and light are better utilised. Thus bushy, shrub-like, and dendroid thalli arise; these in the Algae have often delicate branches moving with the surrounding water, to which they offer little resistance.

In branching the apex of the young plant may divide into two new and equivalent parts (DICHOTOMOUS BRANCHING), as happens repeatedly in the fan-shaped thallus of the Brown Seaweed, *Dictyota dichotoma* (Fig. 80; cf. the diagram in Fig. 79 *a*). In other branched forms there is a new formation of growing points which give rise to lateral branches (LATERAL BRANCHING), and in the higher forms this becomes more and more limited to the apical region of the thallus; the youngest and shortest lateral branches are the nearest to the apex. Such an ACROPETAL origin of new lateral members is already evident in the filamentous Green Alga, *Cladophora* (Fig. 81; cf. also Fig. 86). In the simplest case of lateral branching a single main axis (MONOPODIUM) continues its apical growth throughout the branch system. It behaves as the parent-axis to a large number of lateral axes, arising successively on all sides. These grow less actively than the main axes but can in turn branch similarly. This type of branching is called RACEMOSE (cf. the diagram, Fig. 79 *b*).

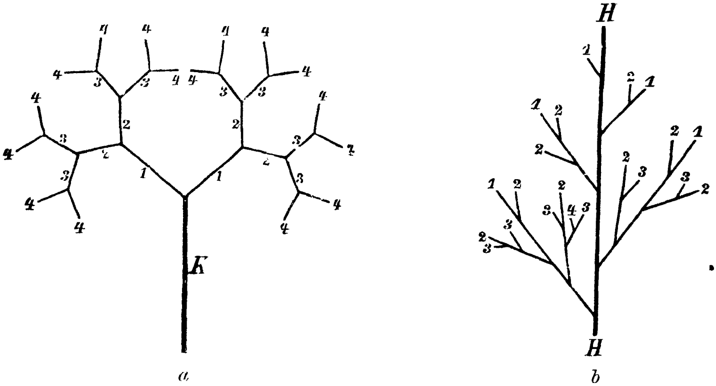

FIG. 79.—*a*, Diagram of dichotomous and, *b*, of lateral racemose branching. *K*, Axis of the young plant; *H*, main axis; *1*, *2*, *3*, *4*, daughter-axes of corresponding orders.

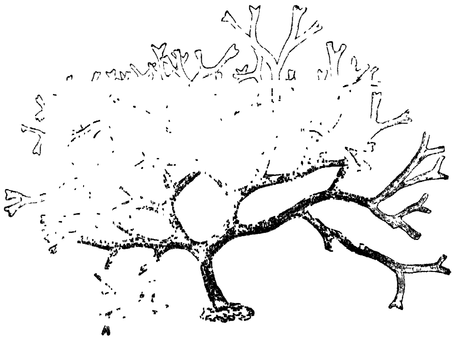

FIG. 80.—*Dictyota dichotoma*. (⅔ nat. size. After SCHENCK.)

Cymose branching, which will be described in connection with the cormus, also occurs in Thallophytes.

All lateral axes which arise on the axis of the young plant are spoken of as branches of the first order; those which, in turn, arise on branches of the first order as of the second order, and so on (cf. Fig. 79). The axis on which a daughter-axis arises is termed relatively to it a parent-axis. Parent-axes may thus themselves be daughter-axes of the first, second, third, etc., orders. The lateral axes may have unlimited growth (LONG SHOOTS), or may have the form of SHORT SHOOTS with limited growth.

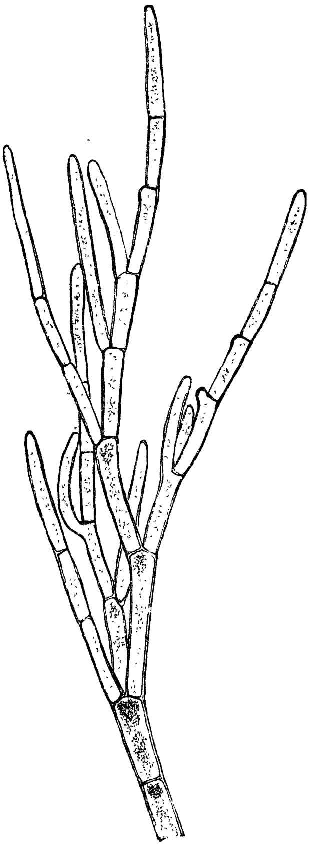

FIG. 81.—Portion of *Cladophora glomerata*. (× 48. After SCHENCK.)

In contrast to the TRUE BRANCHING described above, what is known as FALSE BRANCHING is found in some low filamentous Algae and Bacteria. It comes about by the filament breaking into two portions, still, however, held together by the mucilaginous sheath; each new end arising by the rupture can grow on as a filament (Fig. 82). When an unbranched thallus is subsequently split into a number of lobes, as in the case of the flat thallus of *Laminaria* (Fig. 359), the term branching is not used.

The thallus in the Fungi, which do not assimilate carbon dioxide, has a correspondingly peculiar aspect. It is termed a MYCELIUM, and consists of thin, highly-branched, cylindrical, colourless filaments (Fig. 83 and Fig. 6) called HYPHAE. These penetrate the substratum, such as the humus soil of a wood, in all directions and thus expose a large surface for the absorption of the necessary food-materials. Parasitic fungi, if not inhabiting the cells, usually send suctorial projections of the hyphae (haustoria) into the living cells of the host plant from the hyphae in the intercellular spaces (Fig. 84).

7. Division of Labour between the Branches of the Thallus.—The most highly-segmented types of thallus are met with in some Siphoneae and in the Brown and Red Seaweeds (Phaeophyceae and Rhodophyceae). The external segmentation of some of these resembles in a remarkable manner the shoot in cormophytes. Some of these Algae attain a great size, the thallus of the Brown Alga, *Macrocystis*, being over 45 m. long. A good example of high differentiation is afforded by the Red Seaweed, *Delesseria sanguinea* (Fig. 85), which has leaf-like lateral branches seated on the cylindrical, branched, relatively main axes. In many such forms, besides the formation of attaching organs or haptera and of branches, a further degree of differentiation is attained. Some cylindrical branches continue the growth and branching of the thallus as LONG SHOOTS. Other branches borne on these are SHORT SHOOTS with limited growth, and serve as leaf-like ORGANS OF ASSIMILATION. These short shoots may again exhibit a division of labour among themselves. Such forms are of the greatest interest morphologically, as they show how the leaves of cormophytes could have arisen from short shoots.

Leaf-like short shoots have evidently arisen independently in a number of series of thalloid plants. Thus the leaf-like branches of the Siphoneae and Brown Algae are not homologous with those of the Red Algae but only analogous.

8. Internal Structure of the Thallus.—Thalli, whether segmented or unsegmented, may consist of a single protoplast (*e.g.* Siphoneae, *Caulerpa*, Fig. 343) or more usually of many cells. In the latter case the cells are arranged in filaments (Fig. 81), surfaces, or are united to form a cell-mass. The simplest multicellular thalli are composed of uniform cells all capable of division. As soon as a growing point is defined a distinction between MERISTEMATIC and PERMANENT cells is apparent.

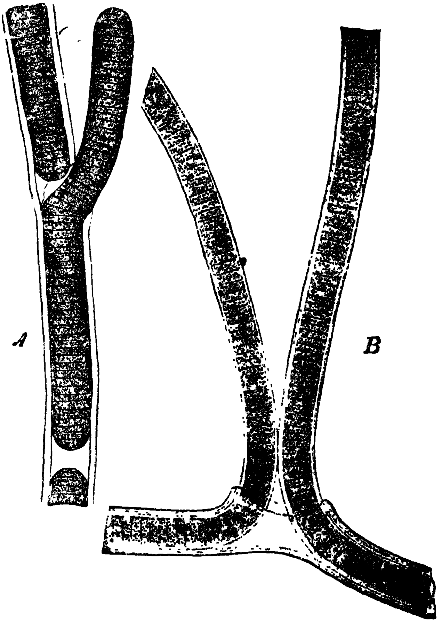

FIG. 82.—False branching in Cyanophyceae. *A*, *Plectonema Wollei*; only the upper end of the broken filament grows out as a branch. *B*, *Pl. mirabile*; both ends proceed to grow. (OLTMANNS after KIRCHNER and BORNET.)

The extreme tip of the apical growing point is nearly always occupied by a single cell termed the APICAL CELL. This sometimes differs little from the other cells, as in the case of *Cladophora glomerata* (Fig. 81). The dome-shaped apical cell is, on the other hand, prominent on the multicellular long shoots of the Brown Alga, *Cladostephus verticillatus* (Fig. 86). Such an apical cell divides by transverse walls parallel to one another, which cut off disc-shaped segments from its lower end. These divide further in a regular way, first by longitudinal and then by transverse walls into a number of cells, which are at first meristematic. The lateral branches, mostly developed as shoots of limited growth, develop from lateral cells in acropetal succession, and give the characteristic form to the plant (Fig. 86). Flat ribbon-shaped thalli may have a similar but correspondingly flattened apical cell, as seen in the Brown Seaweed, *Dictyota dichotoma* (53) (Fig. 87). Flat segments are cut off from this by walls convex backwards, and are then divided by longitudinal walls. Sometimes the apical cell is divided by a longitudinal wall into two cells of equal size lying side by side (Fig. 87 *B*, *a*, *a*), each of which forms one of the branches of the dichotomy.

The permanent cells even of highly-differentiated thalli almost always have the characters of parenchyma.

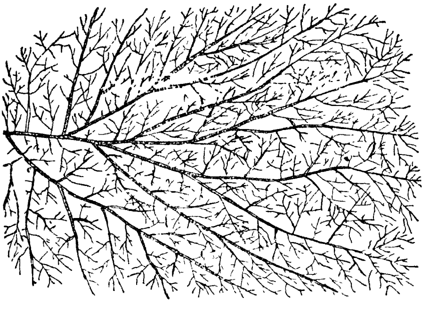

FIG. 83.—Portion of the mycelium of *Penicillium*. (× about 35.)

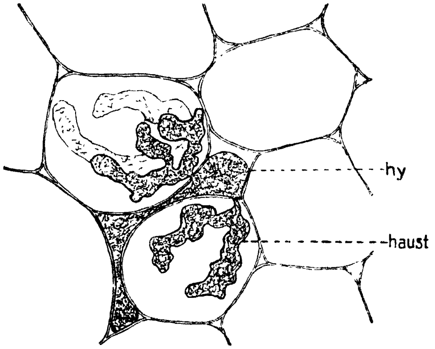

FIG. 84.—Haustoria (*haust*) of *Peronospora parasitica* in parenchymatous cells of *Capsella*. *hy*, The intercellular hyphae. (× 240.)

In a multicellular thallus there may be a distinction of peripheral assimilatory parenchyma with abundant chlorophyll, storage parenchyma, colourless and with abundant reserve materials, and conducting parenchyma composed of elongated cells.

Since the multicellular Algae living in water do not require protection against drying up, and when exposed to the air at ebb-tide are protected by a covering of mucilage, a typical epidermal layer is wanting. The Algae show, however, an outer lamella of the cell-walls of their superficial cells, which stains brown with chlor-zinc-iodide. Rigidity of the thallus, especially in forms that grow exposed to the surf, is provided for by thickening of the walls of the outer layers of cells and sometimes by incrustation with calcium carbonate. In the Bladder Wrack (*Fucus vesiculosus*) special mechanical cells, characterised by their thickened walls and their great extensibility and elasticity, are present. The Laminarieae, which are also Brown Algae, attain the highest grade of internal differentiation. The cortex frequently contains mucilage-canals, and the medulla has rows of cells resembling sieve-tubes and serving for the transport of materials. The axis grows in thickness by the continued division of a cortical layer, which forms concentric zones of secondary tissue, recalling the annual rings of the higher plants.

(b) Bryophyta (54).—The fact that the Mosses and Liverworts (Bryophyta) assimilate carbon dioxide finds expression in their external form and internal structure. There are Liverworts such as *Riccia fluitans* (Fig. 88) in which the dichotomously-branched ribbon-shaped body resembles the thallus of *Dictyota* (Fig. 80). In *Blasia pusilla*, another Liverwort (Fig. 89), the ribbon-shaped thallus has a midrib and bears lateral lobes as if the separation of leafy structures was commencing. The most completely segmented Liverworts, such as *Plagiochila asplenioides* (Fig. 90), and all the Mosses have cylindrical branched stems bearing such leaves as organs of assimilation. The lateral branches stand beneath the leaves on the main axis. These dorsiventral, bilateral, or radially-symmetrical leafy stems are only analogous to the shoots of the higher plants and are best regarded as highly-differentiated thalli. Though these plants, in contrast to the Algae, are mostly sub-aerial organisms they do not possess true roots, but are attached to the soil by RHIZOIDS. These are unicellular hairs, separated from the basal cell bearing them by a wall, or branched filaments of cells, and serve to absorb water. Many of these plants can absorb water by their whole surface.

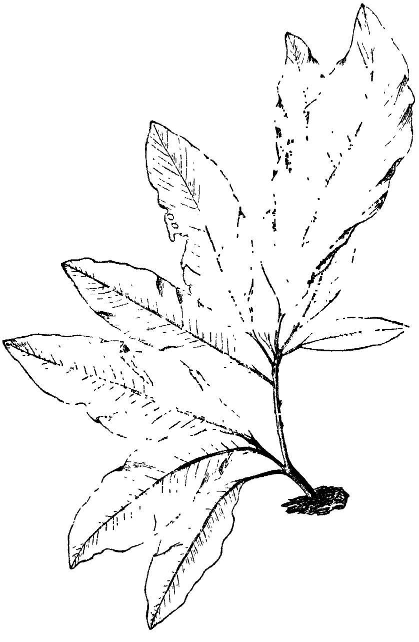

FIG. 85.—*Delesseria sanguinea.* (½ nat. size. After SCHENCK.)

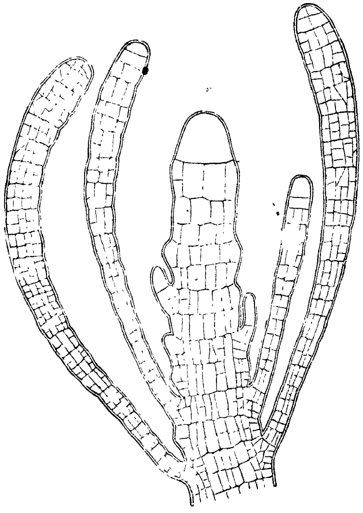

FIG. 86.—*Cladostephus verticillatus.* (× 30. After PRINGSHEIM.)

In the Bryophyta, which are all multicellular, the summit of the apical growing point is frequently occupied by a single apical cell. In ribbon-shaped Liverworts, such as *Metzgeria* and *Aneura*, as in some similarly-shaped Algae, the apical cell is wedge-shaped (Fig. 91), and cuts off segments in two rows. The segments are cut off by oblique walls inclined alternately to the right and left. By further division the segments give rise to the body of the plant. The apparently dichotomous branching of Liverworts with growing points of this type can be traced back to the early delimitation of a new apical cell in the acroscopic half of a young segment (Fig. 91 at *b*). In the erect radially-constructed thalli of the Mosses the apical cell has the form of a three-sided pointed pyramid, and cuts off three rows of segments. The young leaves of the Mosses grow at first by a two-sided apical cell, but later have intercalary growth.

The permanent tissues reach a higher level of differentiation than in the Algae. This is connected with the special conditions which the life on land of the Bryophyta introduces. There is only rarely a definite epidermis in which a typical stomatal apparatus may be differentiated, though the superficial cells are covered by a kind of cuticle. In some Mosses there are in addition elongated and pointed mechanical cells which closely resemble sclerenchyma fibres.

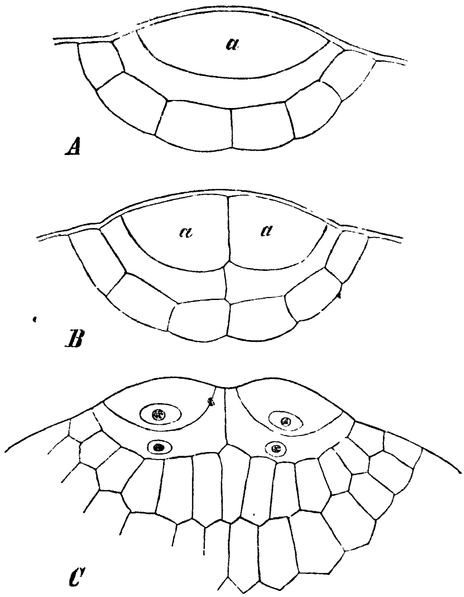

FIG. 87.—The growing point of *Dictyota dichotoma*, showing the dichotomous branching. *A*, Initial cell. (× circa 500. After E. DE WILDEMAN.)

Some Bryophytes have a strand of elongated cells serving for conduction. This is situated in the midrib of the ribbon-shaped forms. Conducting strands clearly limited from the surrounding tissue are first met with in the Mosses (cf. Fig. 92).

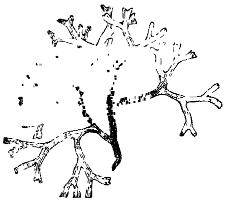

FIG. 88.—*Riccia fluitans*. (Nat. size. After SCHENCK.)

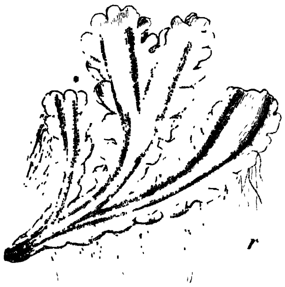

FIG. 89.—*Blasia pusilla*. *r*, rhizoids. (× 2. After SCHENCK.)

The most perfect strands of this kind are found in the stems of the Polytrichaceae. They contain elongated, thin-walled, water-conducting elements, thick-walled mechanical tissue, and elongated cells that contain proteids and starch. Strands of similar construction are also found in the thick midribs of the leaves and are connected with that of the stem.

(c) Gametophyte of the Cormophytes (54). In the developmental history of the cormophytes a stage with a thalloid vegetative body occurs. Two generations alternate regularly with one another (cf. p. 191), the spore-bearing plant or SPOROPHYTE and the sexual plant or GAMETOPHYTE. The vegetative body of the former is a cormus, while that of the latter is usually a very simply segmented and constructed thallus (prothallium). In Pteridophyta the gametophyte is usually a flat green structure attached to the soil by rhizoids and living independently (Fig. 93). It is at most a few centimetres in length and resembles a small Liverwort thallus.

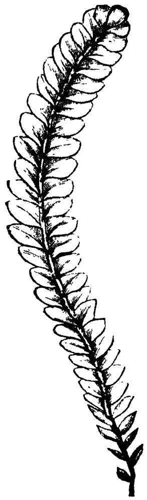

FIG. 90. – *Plagiochila asplenioides*. (Nat. size. After SCHENCK.)

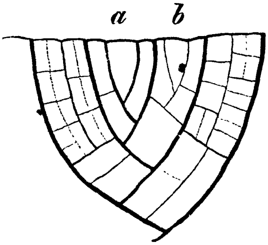

FIG. 91.—Diagrammatic representation of the apex of *Metzgeria furcata* in process of branching, viewed from the dorsal side. *a*, Apical cell of parent shoot; *b*, apical cell of daughter shoot. (× circa 370. After KNY.)

B. THE CORMUS (55)

The cormus is divided into shoot and root, the shoot into the stem and the leaves. Stems, leaves, and roots are thus the fundamental organs of the cormus, which evidently is adapted to life on land by its outer and inner construction.

As in many thalli the surface of the cormus is considerably increased by branching. The shoot forms lateral branches, the roots give rise to lateral roots, and by this branching, which in many plants begins even in the embryo, a SHOOT-SYSTEM and ROOT-SYSTEM arise.

The term cormus is usually employed as equivalent to shoot to denote a leafy stem apart from the roots, and a shoot or cormus is then recognised in the leafy Bryophyta. There are grounds for thinking that the "shoot" of the Moss is not homologous with the shoot of the higher plants. It is therefore advisable not to employ the terms shoot or cormus in speaking either of the Bryophyta or of similarly organised "leafy" Algae. There is nothing to prevent using the conception of the cormus as a wider one than that of the shoot, and understanding by it the vegetative organs of the cormophytes differentiated into shoots and roots. Further, there are transition forms between roots and shoots (*e.g.* the rhizophores of *Selaginella*) and between leaves and shoots (*e.g.* in *Utricularia*).

1. Construction of the Typical Cormus

The fundamental organs of those cormi which can be regarded as typical will be considered in the first place. Their peculiarities appear typically in such plants as our native trees, or even more clearly in many herbs. The fundamental organs may undergo many modifications and, in extreme cases, their distinction may be difficult.

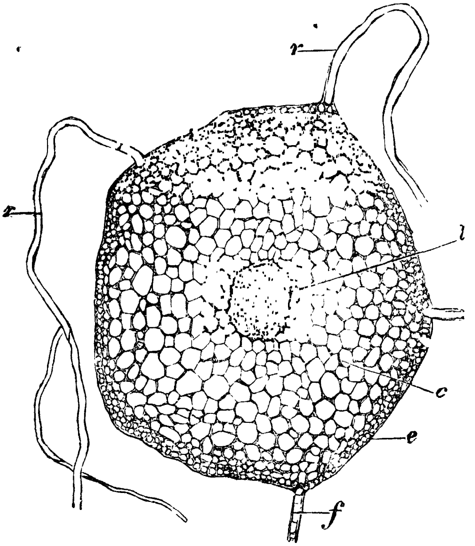

FIG. 92.—Transverse section of the stem of *Mnium undulatum*. *l*, Conducting-bundle; *c*, cortex; *e*, peripheral cell layer of cortex; *f*, part of leaf; *r*, rhizoids. (× 90. After STRASBURGER.)

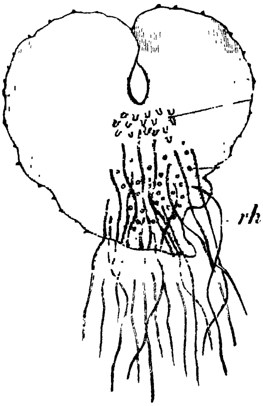

FIG. 93.—*Aspidium filix mas.* Prothallium from the lower side. *rh*, rhizoids. (× about 8. After SCHENCK.)

(a) The Shoot (56)

The shoot in land-plants may be wholly or in part exposed to the air (AERIAL SHOOT) or be partly buried in the soil (SUBTERRANEAN SHOOT, Fig. 139); the latter is the case in many perennial herbaceous plants (cf. Figs. 121, 139). It consists of the STEM or AXIS of the shoot and the LEAVES. The latter on the aerial shoots, which are usually green, are developed as foliage leaves, while on the white or colourless subterranean shoots (root-stocks or RHIZOMES) they are pale scales. The stem bears the leaves and provides for the extension of the shoot-system; this involves the elongation of the stem and the formation of new leaves and lateral branches, the connection between the leaves and roots, and the conduction of material between these organs. The stem in most subterranean shoots further serves as a place of storage of reserve materials. The foliage leaves, like the leaf-like branches of thalloid plants, are the organs of assimilation and transpiration in the cormophytes. The external form and internal structure of the foliage-leaves and stem stand in relation to these functions.

(*a*) **The Growing Point.**—The shoot grows by means of an apical growing point situated at the extreme tip of the stem. Since the growing point is extremely small and scarcely visible to the naked eye, it is best seen when longitudinal sections of the apex of the shoot are examined with a magnifying glass (Fig. 94). It then appears flat or convex (Fig. 94 *v*), and sometimes distinctly conical (Figs. 96, 98). The rudiments of the leaves (*f*) and of lateral branches (*g*) arise laterally beneath the tip and appear as closely-crowded exogenous projections or bulges of the surface. The leaves arise in acropetal order and become larger on passing farther from the apex, as is clearly shown in transverse sections of the growing point (Fig. 95). The growing point and the young leaves, which only arise from the embryonic part of the apex, both consist of meristematic tissue.

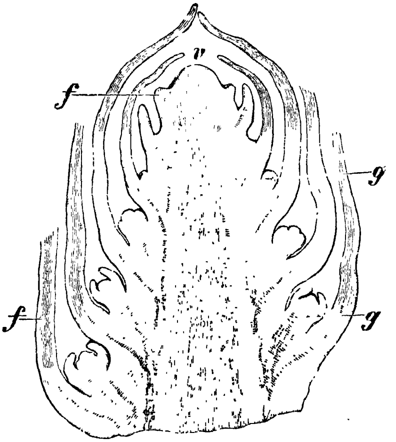

FIG. 94.—Apex of a shoot of a phanerogamic plant. *v*, growing point; *f*, leaf-rudiment; *g*, rudiment of an axillary bud. (× 40. After STRASBURGER.)

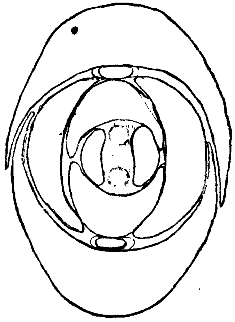

FIG. 95.—Apical view of the growing point of a shoot of *Euonymus japonica*. (× 12. After STRASBURGER.)

In the majority of the Ferns and in the Horsetails a single apical cell is found at the summit of the growing point (Fig. 96 *t*). It has the form of a three-sided pyramid (tetrahedron) with a convex base. The apical cell (Fig. 96 *t*, 97) of the main shoot of the Common Horsetail (*Equisetum arvense*) will serve as an example. Viewed from above (Fig. 97) it appears as an equilateral triangle in which new walls (*p*) are successively formed parallel to the original walls. Each segment (S', S'') becomes further divided by partition walls (*m*). In the Pteridophyta which have apical cells the leaf rudiments (*f*, *f'*, *f''*) usually commence their development with an apical cell which cuts off two rows of segments (*f*). The activity of this usually ceases, and the development of the leaf is continued by marginal growth due to a number of equivalent two-sided cells. This is the case, for example, in *Equisetum*. The lateral buds (*g*) also start from a single cell that becomes the apical cell.

In the Lycopodiaceae, among the Pteridophyta, and in Phanerogams, there is no such single apical cell at the growing point. In place of this a number of equivalent meristematic cells, which often form regular concentric layers (Fig. 98), are met with.

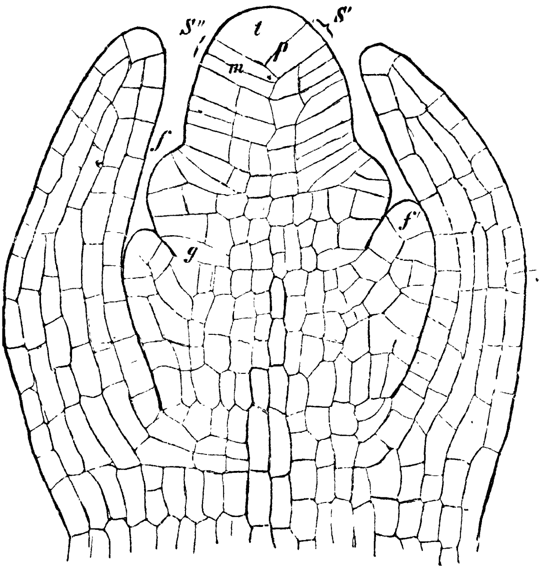

FIG. 96.—Median longitudinal section of the vegetative growing point of *Equisetum arvense*. Explanation in the text. (× 240. After STRASBURGER.)

The outermost layer of cells which covers the growing point and also the developing leaves is termed the DERMATOGEN (*d*) because it gives rise to the epidermis; it usually divides by anticlinal walls only. The cells in which the central cylinder of the stem ends at the apex form the PLEROME (*pl*), while the layers between this and the dermatogen constitute the PERIBLEM (*pr*). The limit between the periblem and plerome is often indistinct.

On such growing points without apical cells the leaves and lateral branches arise as multicellular projections (Fig. 98), which come about by local increase in number of periblem cells, while the dermatogen undergoes anticlinal divisions only and keeps pace with the enlargement (57).

BUD.—The formation of new members at the growing point is followed by their increase in size and differentiation. This applies in the first place to the young leaves, the growth of which exceeds that of the stem apex and is most marked on their lower sides. As a result of this the older leaves close over the growing point (Fig. 94) and the younger leaf rudiments. The growing point thus becomes a BUD in which the delicate younger structures are protected against desiccation by the older and larger, though still immature, leaves. A bud is thus the young incompletely-developed end of a shoot.

VERNATION AND AESTIVATION.[1]—A section through a winter bud shows that the young leaves are fitted in various ways to the narrow space in which they are confined. They may be so disposed that the separate leaves are spread out flat, but more frequently they are folded, rolled (Fig. 99 *l*), or crumpled. The manner in which each separate leaf is disposed in the bud is termed VERNATION. On the other hand, the arrangement of the leaves in the bud with respect to one another is designated AESTIVATION. In this respect the leaves are distinguished as FREE when they do not touch, or VALVATE when merely touching, or IMBRICATED, in which case some of the leaves are overlapped by others (Fig. 99 *k*). If, as frequently occurs in flower-buds, the margins of the floral leaves successively overlap each other in one direction, the aestivation is said to be CONTORTED.

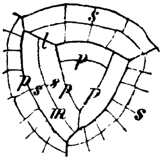

FIG. 97.—Apical view of the vegetative cone of *Equisetum arvense* ; *l*, lateral walls of the segments. Further explanation in text. (× 240. After STRASBURGER.)

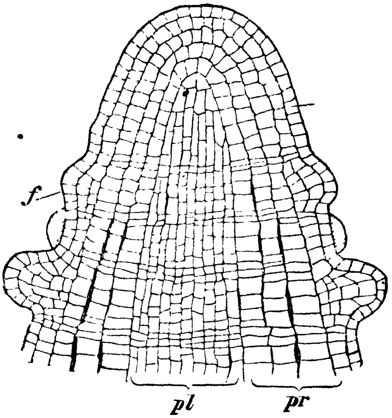

FIG. 98.—Median longitudinal section of the vegetative cone of *Hippuris vulgaris*. *d*, Dermatogen ; *pr*, periblem ; *pl*, plerome ; *f*, leaf-rudiment. (× 240. After STRASBURGER.)

(β) The Axis of the Shoot. A. External Construction.—The active elongation of the stem begins at some distance from the growing point; with this the leaves in the bud begin to separate. It is characteristic of shoots, especially aerial shoots, that this elongation is not limited to a short region below the bud but extends many centimetres (to more than 50 cm.) from this. It is not of course so active in the successively distant zones. The elongation may, on the other hand, be so slight that the mature leaves of the shoot adjoin one another without leaving any free surface of stem between them. As a rule, however, its amount and distribution is such that the insertions of the leaves become separated by bare regions of stem (Fig. 111). These are known as INTERNODES, while the transverse zones of the stem where the leaves are inserted are the NODES. The growth in length is much less in the nodes than in the internodes. In the latter it is often limited to a narrow zone, for example at the base of the internode in the Grasses. There are then a number of zones of intercalary growth in the stem separated by fully-grown regions. The nodes may be swollen (cf. Labiatae).

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[1] [The use of these terms in the following paragraph differs from that customary in England. By VERNATION is understood the arrangement of the leaves in a vegetative bud as a whole. The folding of each individual leaf in the bud is termed PTYXIS. The term AESTIVATION is applied to the arrangement of the parts in a flower-bud.—TRANS.]

In aerial shoots the internodes are usually thin, while they are frequently very thick in subterranean shoots.

The length of successive internodes of an axis exhibits a certain regularity. Usually it increases on ascending a main axis and then diminishes.

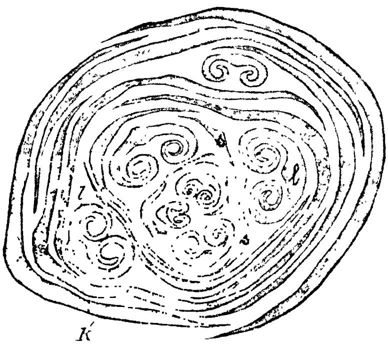

FIG. 99.—Transverse section of a bud of *Populus nigra*. *k*, Bud-scales showing imbricated aestivation [vernation]; *l*, foliage leaves with involute vernation [ptyxis]; *s*, each leaf has two stipules. (× 15. After STRASBURGER.)

Leaf Arrangement (58).—The distribution or arrangement of the leaves is very characteristic of shoots, and exhibits great variety. One or a number of leaves may be borne at each node. When there are several leaves they form a WHORL and are termed the members of the whorl, while the leaf arrangement is spoken of as VERTICILLATE. When there is only one leaf at each node the arrangement is ALTERNATE.

A very remarkable and peculiar regularity is exhibited by the arrangement of leaves on all sides of erect shoots; it is often at once evident when the growing point is looked at from above (Figs. 95, 100). The youngest leaf-rudiments adjoin the older ones in such a way as to best utilise the available space. The relations of position are best shown when they are plotted diagrammatically on a ground-plan. The position of the leaves is represented in the diagram, which is of a plane at right angles to the axis of the stem, as if the latter were conical and viewed from the tip; it is thus possible to indicate a higher position on the stem by a more internal position in the plan. Such ground-plans of leaf arrangements are called DIAGRAMS (Fig. 101). The centre corresponds to the apex of the stem; the leaves nearest to this are the youngest or uppermost, and those farther out are successively older and lower. It is convenient to indicate each node by a circle; when there are several leaves at the same node they are represented on the same circle. Such diagrams agree with the figures of transverse sections of a bud in the neighbourhood of the apex of the stem (Figs. 95, 100).

It thus appears that THE LEAVES ON AN ERECT RADIAL SHOOT ARE DISPOSED AS REGULARLY AS POSSIBLE AROUND THE STEM. THIS ENSURES THAT THE EXPANDED LEAVES DO NOT SHADE ONE ANOTHER BUT MAKE THE FULLEST POSSIBLE USE OF THE LIGHT. The distribution is so regular that the angle between two successive leaves (*e.g.* in Fig. 101, leaves 1 and 2, 2 and 3, etc.) is constant; this is termed the ANGLE OF DIVERGENCE, or, when expressed as a fraction of the circumference, the DIVERGENCE. It is different in different kinds of plants.

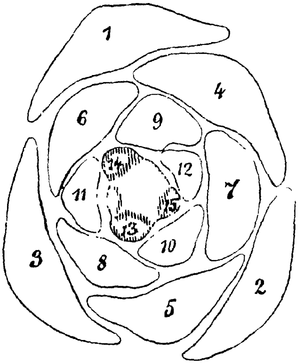

FIG. 100.—Transverse section of a leaf-bud of *Tsuga canadensis*, just below the apex of the shoot, showing a $\frac{5}{13}$ divergence. (× circa 20. After HOFMEISTER.)

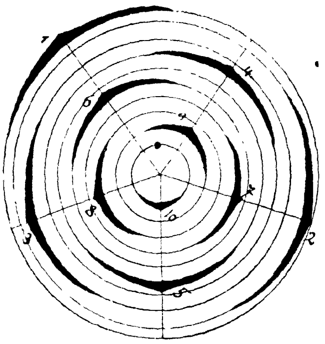

FIG. 101.—Diagram showing $\frac{2}{5}$ position of leaves. The leaves numbered according to their genetic sequence. (After STRASBURGER.)

In the case of verticillately-arranged leaves the angle of divergence of a whorl (Fig. 102) is the circumference divided by the number of leaves, which is usually the same in each whorl. The members of successive whorls do not stand immediately above one another but alternate, so that the members of one whorl come above the intervals between those of the whorl below (Fig. 95, 102). The result of this arrangement, combined with the equality of the angle of divergence in each whorl, is that the leaves of such a shoot are arranged in twice as many vertical rows as there are members in each whorl (Fig. 102). These longitudinal or vertical ranks are termed ORTHOSTICHIES. A frequent case of verticillate arrangement is that of whorls of two members (Figs. 95, 102). In this arrangement, which is termed DECUSSATE, the angle of divergence is 180°; the divergence is thus $\frac{1}{2}$, and there are four orthostichies. If there are three members in a whorl the angle of divergence is 120°, the divergence $\frac{1}{3}$, and there are six orthostichies.

When the arrangement of the leaves is alternate the divergence may be $\frac{1}{2}$ (Fig. 103), $\frac{1}{3}$ (Fig. 145), $\frac{2}{5}$ (Fig. 101), $\frac{5}{13}$ (Fig. 100), etc. Here also, owing to the uniformity of the angle of divergence, the leaves will stand in orthostichies on the stem. With a divergence of $\frac{1}{3}$ leaf 4 will stand vertically over leaf 1 (5 over 2, 6 over 3, 7 over 1, etc.); with a $\frac{2}{5}$ divergence (Fig. 101) leaf 6 comes over leaf 1, 7 over 2, 8 over 3, etc. If one imagines the insertions of successive leaves connected by the shortest line passing round the circumference of the stem, this line will be a spiral. The alternate arrangement of leaves is therefore also spoken of as SPIRAL ARRANGEMENT. The segment of this genetic spiral passing from leaf to leaf till one vertically over the starting point is reached is called a CYCLE of the spiral (*e.g.* in Fig. 101 from 1-6 or 3-8). In the case of $\frac{1}{3}$ divergence the cycle consists of three leaves and passes once round the stem. In $\frac{2}{5}$ divergence (Fig. 101) the cycle consists of five leaves and passes twice round the stem. In the fraction expressing a divergence the numerator shows how often the cycle passes round the stem, and the denominator how many leaves the cycle includes. The latter also indicates how many orthostichies there are and which leaf will next be found in the same orthostichy. For example, in a $\frac{5}{13}$ divergence the stem will be passed round five times before the next superposed leaf is met with, there are 13 orthostichies, leaf 16 stands over leaf 3 (3 + 13), and over leaf 8, leaf 21 (8 + 13). Since the denominator always indicates the number of orthostichies, the $\frac{1}{2}$ divergence is also spoken of as two-ranked, the $\frac{1}{3}$ divergence as three-ranked, etc. When the leaves on a stem are crowded and in contact, another series of ascending spirals becomes more prominent; these are the PARASTICHIES. They come about by the contact of those leaves the lateral distance between which on the axis is the least. The parastichies appear very clearly on pine-cones from which Fig. 104 is prepared as a somewhat diagrammatic view from the base. In this view the parastichies appear as spiral lines. Several systems of parastichies running in the same direction are clearly apparent. One of these (indicated by the unbroken lines I-VIII) goes in the direction of the hands of a clock; two cross this system, one being a flat and the other a steep spiral, and these are marked by the two types of dotted lines. Two systems of equivalent parastichies that cross can be used to determine the divergence (cf. Fig. 104). Denoting any particular leaf by 1, the number of the next leaf in the parastichy is obtained by adding to 1 the number of the oblique ranks of that system which pass round the stem. There are 8 parastichies indicated by unbroken lines, so that the next leaf in this parastichy is 1 + 8 = 9 and the next to this 9 + 8 = 17, etc. Taking the opposite system of spirals there are 5 marked by broken lines (13 marked by dotted lines), and thus the

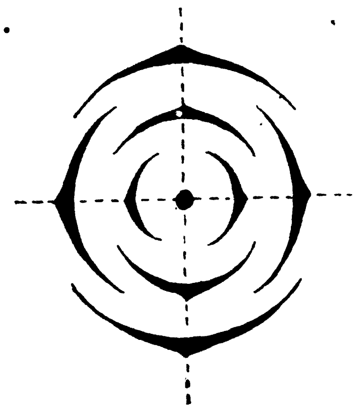

FIG. 102.—Diagram of the decussate arrangement of leaves. The dotted lines are the orthostichies. (Modified after STRASBURGER.)

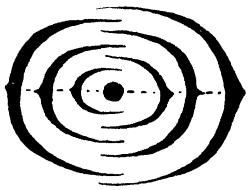

FIG. 103.—Diagram of two-ranked arrangement of leaves. The dotted lines are the orthostichies. (Modified after STRASBURGER.)

leaves in the system with broken lines are $1+5=6$, $6+5=11$, and so on. In the dotted parastichies, on the other hand, they are $1+13=14$, $14+13=27$, etc. This regularity depends on the fact that in every system of parastichies there must be as many leaves between the successive leaves of one parastichy as the remainder of the parastichies of that system. (This, in the system indicated by unbroken lines in Fig. 104, is 7, and seven leaves intervene between 1 and the next leaf of the parastichy. This leaf must follow on $1+7$ and therefore be number 9.) If all the leaves are numbered in this way the successive numbers 1, 2, 3, 4, etc., give the genetic spiral and the divergence. The pine-cone in Fig. 104 has the leaf arrangement $\frac{8}{21}$, and in accordance with this the leaves 1, 22, 43 come above one another—*i.e.* in the same orthostichy. When the divergences are determined in diverse plants with alternately-arranged leaves it is found that certain divergences are particularly common. The series $\frac{1}{2}$, $\frac{1}{3}$, $\frac{2}{5}$, $\frac{3}{8}$, $\frac{5}{13}$, $\frac{8}{21}$, $\frac{13}{34}$, etc., can thus be arrived at. These fractions have an evident connection with one another; the numerator and denominator of each are the sums of the numerators and denominators respectively of the two preceding fractions. The divergences of this series all lie between $\frac{1}{2}$ and $\frac{1}{3}$ of the circumference of the stem. They deviate the less from one another as the start of the series is departed from and approach more and more an angle of 137° 30′ 28″. This series is termed the main series of leaf arrangements. There are also other similar series, but the main series is characterised by the fact that by its divergences the most uniform spacing of the leaves on an axis is attained with the smallest number of leaves. The discoverers of this series were Carl Schimper and Alexander Braun.

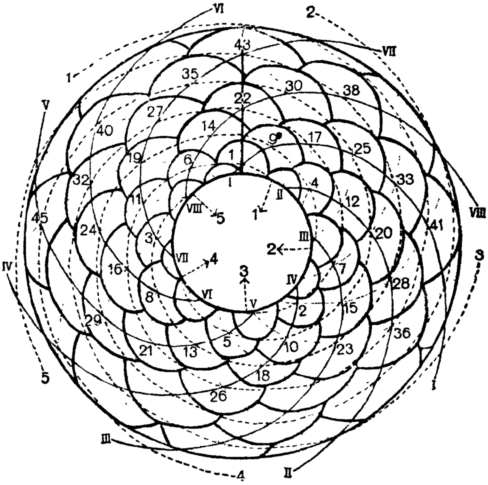

FIG. 104.—Semi-diagrammatic view of a pine-cone seen from below. Divergence of scales $\frac{8}{21}$; I-VIII, system of parastichies running in the direction of the hands of a watch; 1-5, system of parastichies running in the opposite direction. For further description see the text.

Erect radial shoots with elongated internodes or with broad leaves have usually few orthostichies, while those with short internodes and narrow leaves have many. In the latter case the divergences belong to the higher members of the series.

The arrangement of the leaves on inclined dorsiventral stems is relatively simple. A divergence of $\frac{1}{2}$ or a similar arrangement is the most common; by this the leaf surfaces can be placed horizontally and obtain favourable illumination. This is frequently attained by twisting of the internodes, which thus transforms a decussate into a two-rowed arrangement on inclined shoots. Similar changes occur in the case of alternately-arranged leaves in relation to the best utilisation of the light by the leaf-surfaces. The position of the foliage-leaves is nearly always an adaptation to the needs of the plant as regards light. In some horizontal subterranean shoots (*e.g.* of Ferns) the leaves stand in one or two rows on the upper side.

Practically nothing is known of the causes of the regularity in the arrangement of leaves. The assumption of SCHWENDENER that purely mechanical causes acting at the places of origin of the leaves determined the arrangement of the latter has proved to be unfounded (59). The leaves need not arise at the apex in the order of their genetic spiral, nor simultaneously as members of a whorl. Sometimes one side of a growing point may even predominate in the production of leaf-rudiments. The spiral arrangement of the leaf-rudiments on the apex need not be the same as that of the leaves on the fully grown shoot; the divergences on the latter may be the result of secondary displacements.

B. Primary Internal Structure of the Stem (60).—The stem exhibits a much more advanced differentiation of tissues than the long shoots of even the most highly segmented thalli. On the outside a typical EPIDERMIS forms its boundary layer. Beneath this in the internodes (the nodes have a more complicated structure) comes a zone of tissue free from vascular bundles and called the CORTEX. This surrounds the CENTRAL CYLINDER (Fig. 105), as the remaining tissue of the stem including the vascular bundles is called.

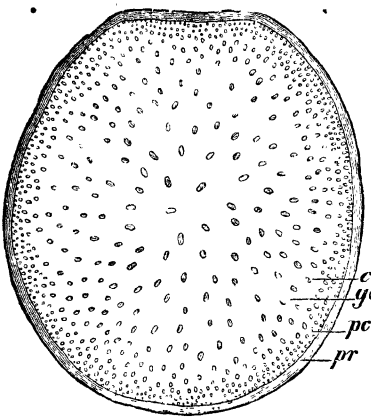

FIG. 105.—Transverse section of an internode of the stem of *Zea Mais*. *pr*, Primary cortex; *pc*, pericycle; *cv*, vascular bundles; *gc*, fundamental tissue of the central cylinder. (× 2. After SCHENCK.)

It is practically desirable to maintain the conception of a central cylinder even though in some Monocotyledons the cortex cannot be clearly distinguished from the central cylinder and the vascular bundles occur close below the epidermis.

Cortex.—The cortex is mainly composed of parenchyma. In green aerial shoots the peripheral layers contain chlorophyll, while those farther in are colourless and serve for storage rather than assimilation. In colourless subterranean stems, which often attain a greater thickness, it is composed of colourless parenchyma which, like the parenchyma of other regions of the rhizome, contains reserve materials. Mechanical tissue is also developed in the cortex. The stem in aerial shoots sustains the weight of the leaves and is exposed to bending by the wind; it must be sufficiently rigid against bending in all directions. Rigidity is attained by the aid of mechanical tissue such as layers or strands of collenchyma or sclerenchyma; this is placed as near to the periphery as possible, sometimes lying just below the epidermis of projecting ridges (Fig. 107, 1, 2).

As SCHWENDENER (44) first showed, the mechanical tissues which render a stem rigid against bending are so arranged as to make the best use of the material. RIGIDITY AGAINST BENDING while the least possible mechanical material is employed is best attained by placing this in a peripheral position. When a straight rod (Fig. 106) is bent the convex side elongates and the concave side is shortened. The outer edges, *a*, *a* and *a'*, *a'*, are thus exposed to the greatest variations in length, while nearer the centre (*i*, *i* ; *i'*, *i'*) the deflection and consequent variations in length are less. If instead of the uniform rod the mechanically effective material were to be disposed as economically as possible, it should be brought close to the periphery. In this position it will oppose the greatest resistance to bending, and if bending takes place will be less easily torn or crushed than less resistant material. Every one knows how great is the resistance to bending of an iron tube, even with thin walls. The builder attains a high level of resistance to bending by placing at the periphery of structures bars of mechanically effective material parallel to one another and to the longitudinal axis of the structure. These are called GIRDERS. It is essential that these GIRDERS should be connected and kept at their proper distances from one another by a sufficiently rigid, but elastic, connecting tissue. Each rod or girder then forms with the one lying immediately opposite a I-girder, the material which occupies the line between the two rods being the connecting material. Were this connection wanting, each rod would be readily bent. In hollow structures, however, it is sufficient that the girders should be joined laterally. In large buildings the peripherally-placed bars have themselves the construction of I-girders, each being constructed of two connected bars.

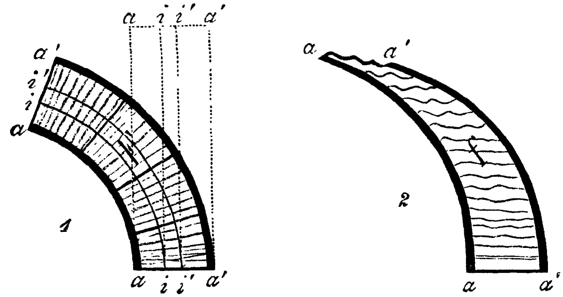

FIG. 106.—1. Longitudinal section of an elastic cylinder, before bending (dotted outline) and after bending (heavy outline). After bending the convex side (*a'*) is stretched and the concave side (*a*) compressed. *f*, Connecting tissue.

2. When the connecting tissue (*f*) is not sufficiently firm, the bands of stereome (*a*, *a'*) curve independently and remain unaltered in length. (After NOLL.)

In many plants in the same way the mechanical tissue forms a peripheral hollow cylinder which may either come next the epidermis or be more deeply situated (Fig. 108 *pc*) ; in others there is a system of similarly-placed strands of mechanical tissue lying side by side (system of simple girders, Fig. 107) ; the latter arrangement may be combined with the complete hollow cylinder (Fig. 107, 2). In other cases each of the peripheral strands has itself the form of a I-girder (Fig. 107, 3) ; only the outer bars of this consist of mechanical tissue, the connection being usually made by a vascular bundle (system of I-girders).

These arrangements are on the whole better shown in the stems of Monocotyledons than in the primary structure of the stems of Dicotyledons and Gymnosperms. In the latter the rigidity can be increased by the secondary thickening.

The innermost layer of cells of the cortex in the mature subaerial stems of land-plants is not usually specially characterised This layer, may, however, be developed as a starch-sheath, or as a typical endodermis (especially in the subterranean shoots of land-plants and in the stems of aquatic plants). If developed as a STARCH-SHEATH its cells contain large, easily-movable starch-grains

Central Cylinder.—This is composed of various tissues. The parenchyma, in accordance with its deep-seated position, is almost or quite colourless, and serves mainly for conduction or storage. The most important parts of the central cylinder are, however, the VASCULAR BUNDLES which serve for transport of substances between the leaves and the root-system

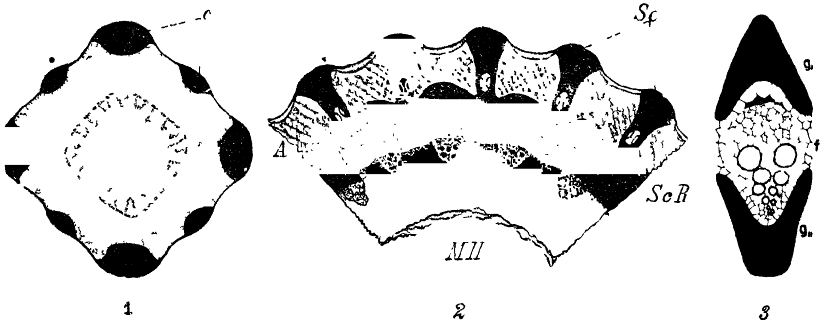

FIG. 107—Rigidity against bending 1. Transverse section of a young twig of *Sambucus*, *c*, collenchyma 2 Part of the transverse section of a haulm of grass (*Molinia coerulea*), *Sc*, ribs of sclerenchyma, *Sc R*, sclerenchymatous ring connecting them laterally *A*, green assimilatory tissue, *MH*, pith cavity 3 Diagram of double girder on a larger scale. *g*, *g*, Girders, *f*, connecting tissue represented by the vascular bundle. (1 and 2 after NOLL)

When the central cylinder and cortex are sharply delimited by a sheath the vascular bundles do not as a rule abut on this, but are separated by a zone one or more layers thick (Fig. 108 *pc*) which is called the PERICYCLE.

There is either only a single vascular bundle in the stem, as in some Ferns and in *Lycopodium* (Fig. 485), or there are a number of vascular bundles. In the latter case the bundles have a definite course and consequently a special arrangement as seen in a transverse section of the stem. In transverse sections of the internodes they appear arranged in a circle in the Horsetails (*Equisetum*) and most Ferns, Gymnosperms and Dicotyledons (Fig. 160). In Monocotyledons (Fig. 105), on the other hand, they are irregularly scattered. If the bundles form a single circle the tissue within this, composed of parenchymatous cells which are alive or may die at an early period, is distinguished as the PITH (*m*). The tissue between the bundles forms the MEDULLARY RAYS (*ms*). This distinction is wanting when the bundles are scattered (Fig. 105).

There are also Ferns (*e.g. Pteridium*, Fig. 484) and Dicotyledons in which the vascular bundles form two (*Cucurbita, Phytolacca, Piper*) or more (*Amarantus, Papaver, Thalictrum*) circles.

The medullary rays may consist of parenchyma, but in a number of herbs their inner portion, between the xylem of adjacent bundles, is formed of sclerenchyma. This contrasts with the outer parenchymatous portions situated in the region of the phloem.

Course of the Vascular Bundles.—In accordance with their functions the vascular bundles form continuous strands which in macerated preparations may be followed from the root-tips to the extremity of the leaves. This can be done by letting herbaceous plants lie in water until all the tissues except the more resistant vascular bundles have decayed and disappeared.

The bundle of the root is traced to the base of the shoot, where it is continuous with the more complicated system of vascular bundles (cf. p. 130). The bundles in the stem may be traceable to the apex without passing into the leaves. Such bundles are termed CAULINE, and contrast with purely FOLIAR bundles which immediately on entering from a leaf unite with cauline bundles.

Thus in the Pteridophyta there may be a network of cauline bundles or a single central bundle (*Lycopodium*, etc.) with which the foliar bundles unite on entering from a leaf-base.

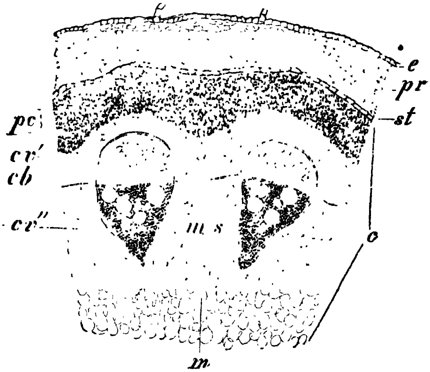

FIG. 108.—Part of transverse section of a young stem of *Aristolochia Sipho*. *e*, Epidermis; *pr*, primary cortex; *st*, starch sheath; *c*, central cylinder; *pc*, pericycle, in this case with a ring of sclerenchyma fibres; *cv′*, phloem, and *cv″*, xylem portions of the vascular bundle; *cb*, cambium ring; *m*, medulla; *ms*, primary medullary ray. (× 48. After STRASBURGER.)

As a rule, however, the bundles of the shoot bend outwards into leaves and are COMMON bundles, the upper portion of which belongs to a leaf and the lower portion to the stem. One or several such bundles pass into a leaf and form collectively what is known as the leaf-trace. The vascular system of the stem in the seed-plants consists as a rule entirely of these leaf-traces or common bundles.

The leaf-trace bundles may remain separate from one another in the stem, but usually each descending bundle of the trace ends by joining another bundle that has entered from a lower leaf. A splitting or forking of the bundle may precede this junction. Such a reticulate arrangement of the bundles ensures a uniform distribution of the water supply, since each bundle of the stem as a consequence of its subdivision provides water to a larger region of the shoot. The general course of the bundles differs in different species according to the length of the free course of the single bundles of the trace, the course they follow, and the subdivision they undergo. The arrangement of the leaves naturally determines the places of entry of the leaf-traces into the stem. Their course in the stem is, however, quite independent of the leaf arrangement, and can be very different for one and the same type of this.

In the Horsetails, the Coniferae, and the Dicotyledons, all the leaf-trace strands penetrate equally deeply into the stem, to pass down this as parts of the characteristic ring of bundles evident in transverse sections. The course of the bundles in the internode can thus be indicated on the surface of a cylinder or represented as if this surface were flattened in one plane. Complications occur at the nodes by the leaf-trace strands being joined by transversely-placed cauline strands; cross connections of later development often occur in the internodes also.

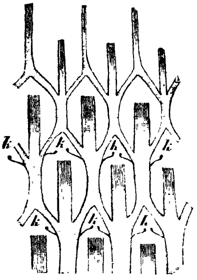

FIG. 109.—Diagram of the course of the vascular bundles in a young branch of *Juniperus nana* shown on the unrolled surface of the cylinder. At *k*, *k* the vascular bundles passing to the axillary shoots are seen. (After GEYLER.)

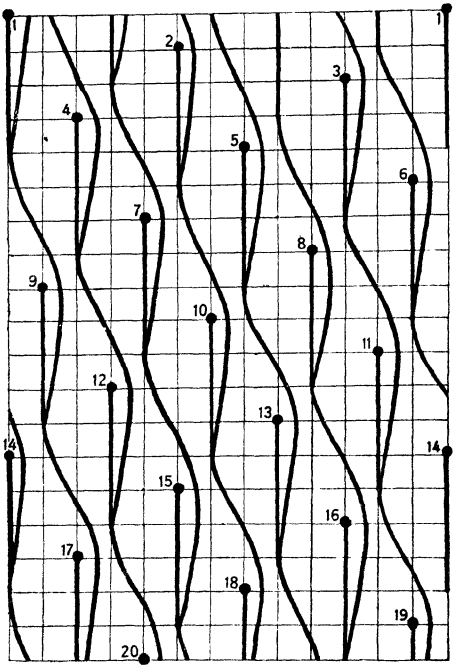

FIG. 110.—Diagrammatic representation of the course of the vascular bundles in a young twig of *Taxus baccata*. The tube of bundles is slit up at 1, and spread out in one plane.

A relatively simple example of the arrangement of vascular bundles is afforded by the young shoots of *Juniperus nana* (Fig. 109), the leaves on which are in whorls of three. From each leaf a leaf-trace consisting of a single vascular bundle enters the stem. This divides into two about the middle of the internode below, and the portions diverge right and left to unite with the adjacent leaf-traces. The arrangement of the bundles in a young twig of *Taxus baccata* as shown in Fig. 110 is less simple, though in this case also the leaf-trace consists of only one bundle. Each leaf-trace can be followed down through twelve internodes before it joins on to another bundle. It first runs straight down for four internodes and then bends aside to give place to an entering trace, with which it later unites. In *Taxus* the leaf insertions, and consequently the places of entry of leaf-traces, have a divergence of $\frac{5}{13}$. An example of leaf-traces composed of three bundles is afforded by young branches of *Clematis viticella*, the arrangement of the leaves on which is decussate. The median strands of the leaf-traces (*a* and *d*, *g* and *k*, *n* and *q*, *t* and *x* in Fig. 111) run down through one internode, dividing at the next node into two arms which fuse with the adjacent lateral strands of the leaves inserted at this node. The two lateral strands of each leaf-trace (Fig. 111 *b*, *c*; *e*, *f*; *h*, *i*; *l*, *m*; *o*, *p*; *r*, *s*) are also free through the internode, but at the node below they curve inwards and become attached to the same lateral strands as the arms of the median bundle of the trace.

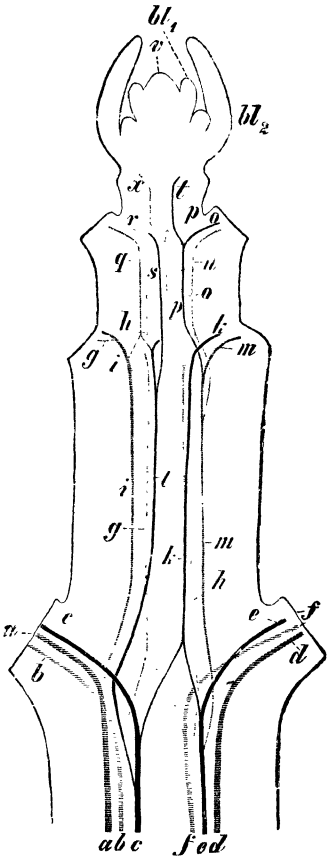

FIG. 111.—*Clematis viticella*. End of a branch which has been made transparent by the removal of the superficial tissues and treatment with caustic potash. The emerging strands have been slightly displaced by gentle pressure. The two uppermost pairs of young leaves (bl^1, bl^2) are still without leaf-traces. *v*, Apical cone. (After NÄGELI.)

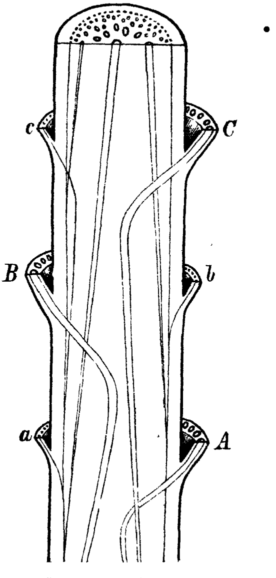

FIG. 112.—Diagrammatic representation of the course of the bundles in the Palm type. Two-ranked leaves encircling the stem are shown cut in their median planes. The leaves (*Aa*, *Bb*, *Cc*) are cut across close to the base; the capital letters indicate the median portion of each. The stem is seen above in transverse section. (After ROTHERT, adapted from ROSTAFINSKI.)

The course of the bundles in the Monocotyledons follows a wholly different type (Fig. 112). The individual bundles of the leaf-trace penetrate to different depths in the stem and thus appear scattered on the cross-section. This results from the prolonged growth in thickness of the growing point after the procambial strand of the first and median bundle of the leaf is laid down. As a result of this the successively-formed procambial strands of the later bundles are placed less deeply. This arrangement is especially well marked in the Palms (palm type), in which each leaf-trace consists of the numerous bundles which pass into the stem from the leaf-base which completely encircles the stem. The median bundle penetrates to the centre of the stem, the lateral bundles, as the median line of the leaf is departed from, less and less deeply. In the longitudinal section of a stem in Fig. 112 only the median bundle for each leaf (*A*, *B*, *C*) and one lateral bundle (*a*, *b*, *c*) are represented. In their further downward course the bundles gradually approach the periphery of the stem, where they fuse with others. The number of internodes which each bundle traverses varies, being greatest for the median bundle.

Structure of the Vascular Bundles (61).—The bundles in the stem are strands of tissue of circular or elliptical outline in cross-section and always consist of xylem and phloem, *i.e.* are complete bundles (cf. p. 64). The sieve-tubes are the most important component of the PHLOEM-PORTION and the water-conducting vessels of the XYLEM-PORTION of the bundle.

In the literature the xylem is frequently also termed wood, vascular tissue, or hadrom ; and the phloem, bast or leptom.

The bundles are variously constructed in different cormophytes. In order to understand the construction of the vascular bundles and the differences between the various types their ontogenetic development must be taken into consideration. The primary vascular bundles are developed from strands of elongated meristematic cells. In these the differentiation of the tissues proceeds gradually over a period of time. So long as the portion of the plant is still growing actively in length the main portion of the strand of meristem remains undifferentiated. Only at limited regions of the strand, usually at the outer and inner margins, are a few elements transformed into permanent tissue. These narrow elements, which are suited to undergo stretching, are on the one hand annular and spiral tracheides, and on the other sieve-tubes with or without companion-cells. They form the PROTOXYLEM and PROTOPHLOEM respectively. Only when growth in length is finished do the bundles become fully differentiated, the differentiation proceeding from the protoxylem and protophloem and resulting in the formation of wider elements (Figs. 116 *B*, 117). The first-formed elements of xylem and phloem have ceased to be functional in the fully-developed vascular bundle. The protoxylem elements are then frequently compressed or torn by the stretching (Fig. 116 B, *l*, at *a*, *a′*, Fig. 118, *rp*), and in some cases their place is taken by a lysigenous intercellular space (Fig. 116 *l*). This is filled with water and thus still serves for water-conduction (62). The walls of the protophloem elements (*cp*) are swollen and their sieve-plates closed by callus.

According to the arrangement of the xylem and phloem a distinction can be made of RADIAL, CONCENTRIC, and COLLATERAL vascular bundles.

In RADIAL vascular bundles (Fig. 113) there are a number of strands of xylem and phloem which, as seen in a cross-section of the circular bundle, stand side by side, alternating with one another. Seen from the side the vascular strands run parallel to one another and to the longitudinal axis of the part of the plant. The strands of xylem may meet in the centre of the bundle and so constitute a star-shaped mass as seen in transverse section. The ends of the rays are made up of the narrowest tracheides (protoxylem), while the vessels towards the centre are always wider (Fig. 113). The strands of phloem are situated in the depressions between the rays, the narrow protophloem elements being at the periphery. One or more layers of parenchyma come between the xylem and the phloem. In radial bundles the differentiation proceeds, in accordance with the position of the first formed elements in the strands of xylem and phloem, from the periphery towards the centre. Radial bundles, though characteristic of roots, occur relatively seldom in stems and are always solitary, as for example in the stems of *Lycopodium*.

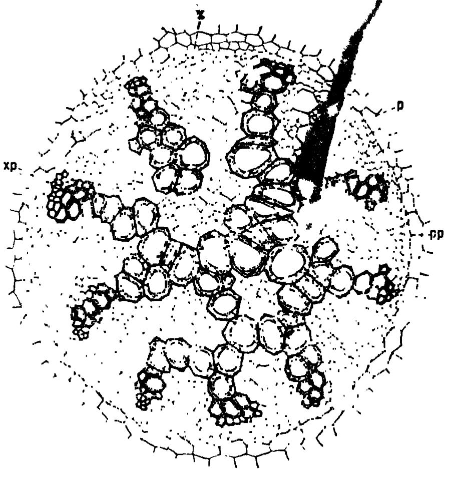

FIG. 113.—Radial vascular bundle from the stem of *Lycopodium Hippuris*. *p*, Phloem; *pp*, primary phloem; *x*, xylem; *xp*, protoxylem. (× 30.)

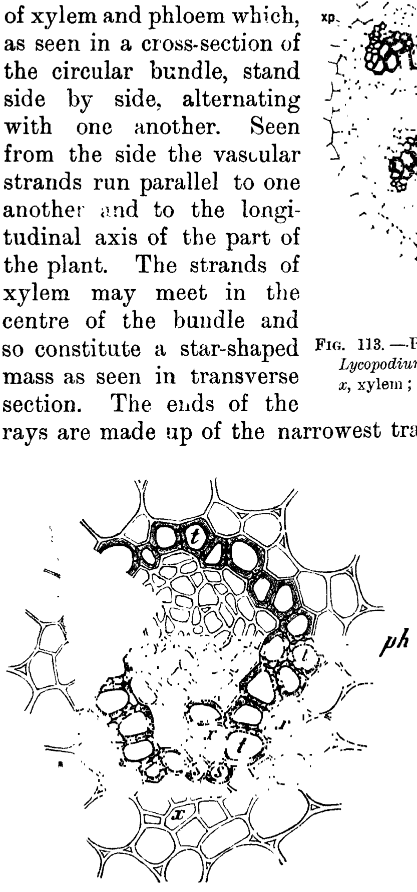

FIG. 114.—Concentric vascular bundle with external xylem from the rhizome of *Convallaria majalis*. *ph*, Phloem; *x*, *t*, xylem; *s*, protoxylem. (After ROTHERT.)

In CONCENTRIC bundles a central strand of xylem or phloem is surrounded on all sides by a cylinder of phloem or xylem. The bundle may be distinguished as concentric with internal xylem when the xylem is centrally placed, and as concentric with outer xylem when this tissue is peripheral. The bundles in the majority of Ferns (Fig. 115) are of the former type, those in the rhizomes or stems of some Monocotyledons (Fig. 114) of the latter. In concentric bundles the development does not follow a single type, and in accordance with this the *position of the protoxylem and protophloem is various.*

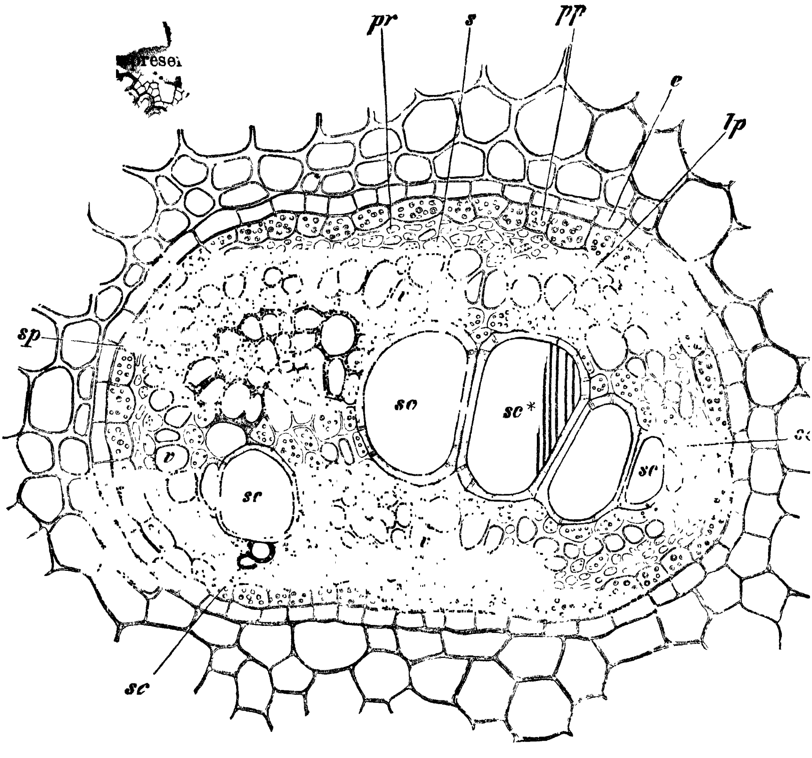

Fig. 115.—Transverse section of a concentric bundle from the petiole of *Pteridium aquilinum*. *sc*, scalariform tracheides; *sp*, protoxylem (spiral tracheides); *sc**, part of a transverse wall showing scalariform perforations; *lp*, xylem parenchyma; *v*, sieve-tubes; *s*, phloem parenchyma; *pr*, protophloem; *pp*, starch layer; *e*, endodermis. (× 240. After Strasburger.)

In the Pteridophytes the narrow elements of the protoxylem (Fig. 115 *sp*) lie in groups in the strand of xylem, peripherally, centrally, or among the later-formed vessels. The xylem is surrounded by a sheath of parenchyma (*lp*). Outside this comes a zone composed of sieve-tubes (*v*) and parenchyma (*s*), the narrow protophloem elements being situated at the outer edge of this.

In COLLATERAL vascular bundles (Fig. 116 *A*), which consist of a strand of xylem and as a rule a single strand of phloem, the xylem lies beside or rather behind the phloem. The median plane of the bundle is always placed radially in the stem, the xylem being directed inwards and the phloem outwards. The protoxylem in collateral bundles is usually placed at the inner edge of the strand of xylem, the protophloem at the outer edge of the phloem, as the bundle is seen in transverse section Such *collateral bundles are characteristic of the* shoots of the Spermaphyta and the Horsetails. BICOLLATERAL

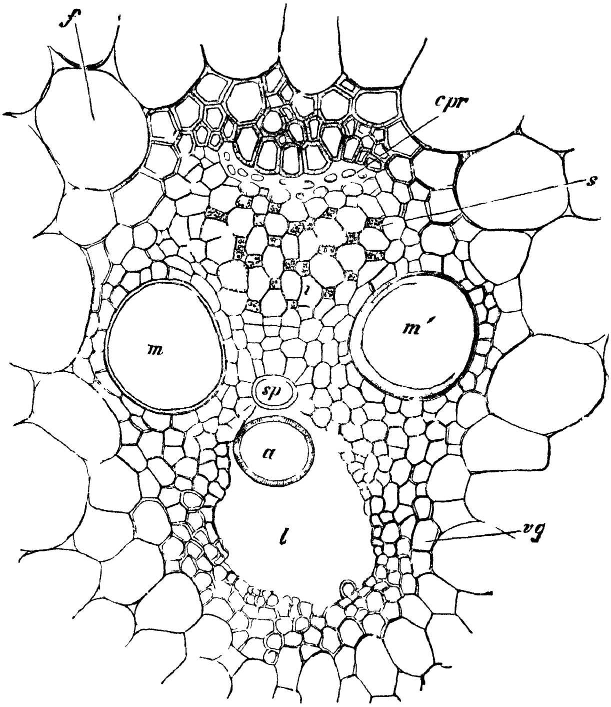

FIG 116 *A*.—Transverse section of a closed, collateral vascular bundle from the internode of a stem of *Zea Mais* *a*, Ring of an annular tracheide, *sp*, spiral tracheide, *m* and *m*, vessels with bordered pits, *v*, sieve-tubes, *s*, companion cells, *cpr*, compressed protophloem, *l*, intercellular passage, *vg*, sheath, *f*, cell of fundamental tissue (× 180 After STRASBURGER.)

bundles, in which the xylem is accompanied by a strand of phloem on the inside as well as on the outside, also occur, as for example in the stems of Cucurbitaceae. In Monocotyledons the collateral bundles, are CLOSED, *i.e.* the whole bundle consists of permanent tissue, the xylem abutting directly on the phloem (Fig. 116 *A*). In Gymnosperms and Dicotyledons, on the other hand, the bundles are usually OPEN, *i.e.* the xylem and phloem remain separated by a layer of meristematic tissue called the CAMBIUM (Fig. 117). In collateral bundles, the elements are developed in succession from the protophloem on the outside and the protoxylem on the inside towards the middle of the bundle. If the meristem is completely used up in this process a closed collateral bundle results; if some remains between the xylem and phloem the bundle is an open one.

It is not at present known what relation holds between the arrangement of xylem and phloem, or the position of the protoxylem and protophloem, and the requirements of conduction in the plant.

In all vascular bundles the strands of XYLEM are mainly composed of narrower or wider lignified elements that serve for the conduction of water. These may be TRACHEIDES and TRACHEAE, or only tracheides. They occur singly or in groups, without intercellular spaces, among narrow, living, elongated and often unlignified cells of the conducting parenchyma (XYLEM-PARENCHYMA), or are surrounded by a sheath of this tissue (Fig. 115 *lp*). In the Pteridophyta only tracheides are present, while in the bundles of Phanerogams both tracheae and tracheides usually occur (Fig. 116 *a*, *sp*, *m*; Fig 118 *rp*, *sp*, *s*, *n*, *t*). In all bundles (cf. Fig. 118) the narrowest vessels are annular or spiral; the others are usually reticulated or pitted, but in the Pteri-

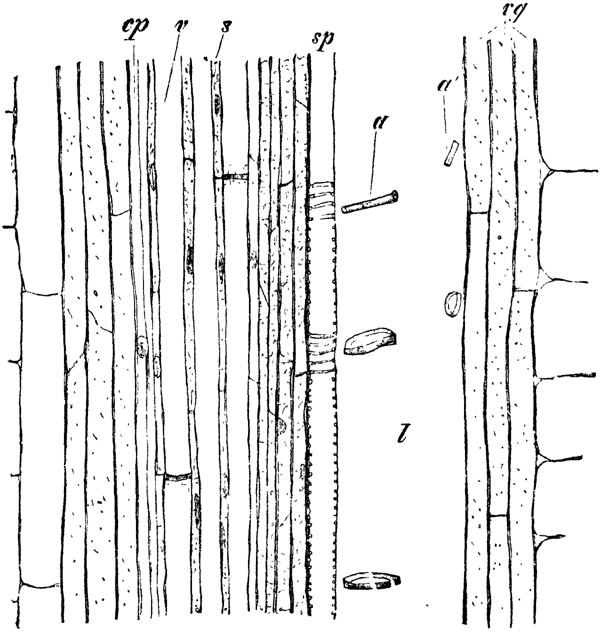

FIG. 116 *B*.—Longitudinal section of a closed, collateral vascular bundle from the stem of *Zea Mais*. *a* and *a'*, Rings of an annular tracheide; *v*, sieve-tubes; *s*, companion cells; *cp*, protophloem; *l*, intercellular passage; *vg*, sheath; *sp*, spiral tracheides. (× 180. After STRASBURGER.)

dophyta the elements, apart from the protoxylem, are scalariform (Fig. 67 *A*).

In the strands of PHLOEM of the vascular bundles (Figs. 115, 116) the SIEVE-TUBES (*v*) are always accompanied by other living cells. These are either the COMPANION-CELLS (Fig. 116 *s*), which are usually shorter than the elements of the sieve-tubes with which they connect by sieve-pits, companion-cells together with other elongated parenchymatous cells (phloem-parenchyma), or PHLOEM-PARENCHYMA only (Fig. 115 *s*). Intercellular spaces are wanting.

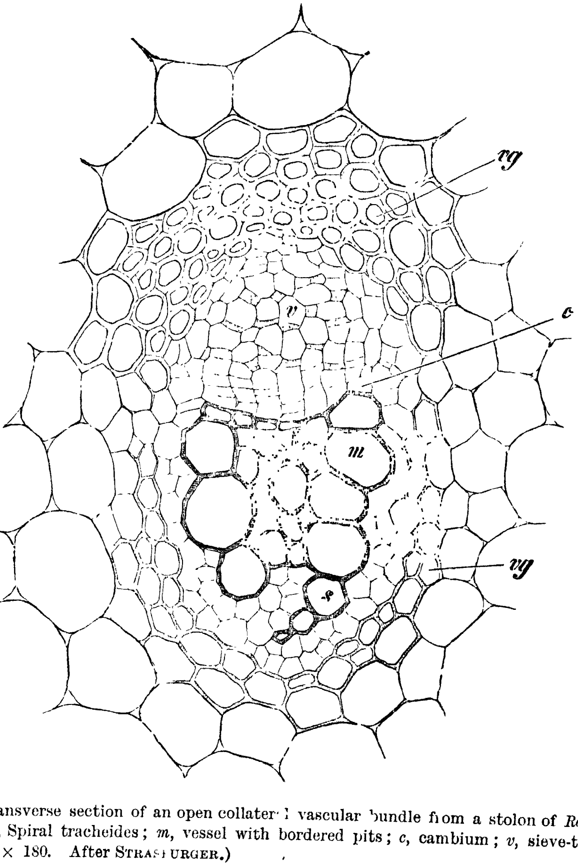

FIG. 117.—Transverse section of an open collateral vascular bundle from a stolon of *Ranunculus repens*. *s*, Spiral tracheides; *m*, vessel with bordered pits; *c*, cambium; *v*, sieve-tubes; *vg*, sheath. (× 180. After STRASBURGER.)

Companion-cells only occur in relation to the sieve-tubes of Angiosperms. They are sister-cells to the members of the sieve-tube, cut off by a longitudinal division, and later undergoing as a rule transverse divisions. They are narrower than the sieve-tubes themselves, and are further distinguished from them by their abundant protoplasmic contents. In some cases laticiferous- or mucilage-tubes occur in the phloem.

The bundle as a whole is often more or less completely surrounded by a BUNDLE-SHEATH. This may have the form of parenchyma without intercellular spaces, the cells often containing large starch-grains (STARCH-SHEATH); in other cases it is sclerenchymatous, or it consists of endodermal cells. It is not regarded as forming part of the vascular bundle itself.

The sheaths frequently serve to limit the conduction of material to the vascular bundle. Sclerenchymatous sheaths are most common at the outer side of the phloem, forming semilunar masses (Fig. 116 *A*, 117 *vg*), and are especially developed in relation to the outermost bundles when these have a scattered arrangement. When a sclerenchymatous sheath surrounds a collateral bundle it is frequently interrupted at the sides, opposite the junction of the xylem and phloem, by parenchymatous or less thickened and lignified elements. These regions facilitate the exchange of water and nutritive substances between the bundle and the surrounding tissues.

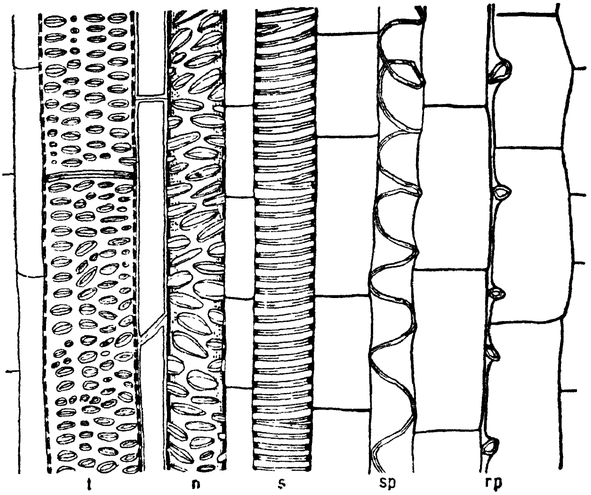

FIG. 118.—Longitudinal section of the wood of a collateral vascular bundle of *Impatiens parviflora*. *rp*, annular thickenings of an annular protoxylem element that is greatly stretched by the growth in length of the stem; *sp*, stretched spiral protoxylem element; *s*, spiral-, *n*, reticulate-, *t*, pitted-vessel. *s*, *n*, *t*, were only fully developed after the growth in length of the stem was completed. (× 120.)

The following conceptions regarding the PHYLOGENY of the types of vascular bundles appear to be established. All the evidence points to the assumption that a stem with a single central vascular bundle is relatively primitive. Such a bundle is found in the stems of a number of living and extinct Pteridophyta and in all roots. The simplest and phylogenetically oldest type of vascular bundle appears to be the concentric bundle with a solid central strand of xylem; at least this appears to be present in the young plants of nearly all existing Ferns (cf. Fig. 119 A). The radial bundle also may be a very ancient type, as is suggested by its constancy in the roots of all living and extinct cormophytes so far as our knowledge extends and in the stems of some cormophytes. No other type of bundle is found in both stems and roots. The variety as regards the construction and arrangement of the bundles, which is met with in the shoots of Pteridophyta as contrasted with the Spermatophyta, leads to speculations upon the mode of origin of these various types of construction from stems with a single concentric bundle. There are stems (Fig. 119 B) in which the vascular tissue of the single central bundle has the form of a hollow cylinder enclosing a central strand of parenchyma or pith (Gleicheniaceae, Schizaeaceae). In others (Fig. 119 E) the hollow cylinder of xylem is lined with an internal zone of phloem (*e.g. Marsilia*). Lastly, there are cases (Fig. 119 F) in which the hollow vascular cylinder is perforated by rhombic leaf-gaps at the departure of the leaf-trace bundles (*e.g. Aspidium filix mas*). In this last case a cross-section of the stem shows a number of typically constructed concentric bundles, with solid central strands of xylem, arranged in a circle. There are also Ferns (Fig. 119 C) in which a cylinder of xylem immediately surrounding the pith is divided by radial plates of parenchyma into a number of longitudinally-running strands of xylem placed side by side, the whole being surrounded by a continuous zone of phloem (*e.g. Osmunda*). Lastly, there are cases (Fig. 119 D) in which the phloem is correspondingly divided, so that the radial plates of parenchyma separate, as medullary rays, the collateral strands composed of xylem and phloem (*e.g.* rhizome of *Ophioglossum*). These examples show how either a reticulate tube of concentric bundles or a hollow tube composed of collateral bundles can be derived from a centrally-placed concentric bundle. If we assume that the phylogenetic development has proceeded on these lines, it is clear that neither one collateral bundle of the Spermatophyta nor one of the circle of concentric bundles found in many Ferns is homologous with the central bundle of "primitively constructed" Pteridophyta. The totality of collateral or concentric bundles in such stems would be homologous with the single central concentric or radial bundle. According to this assumption, which is the essential

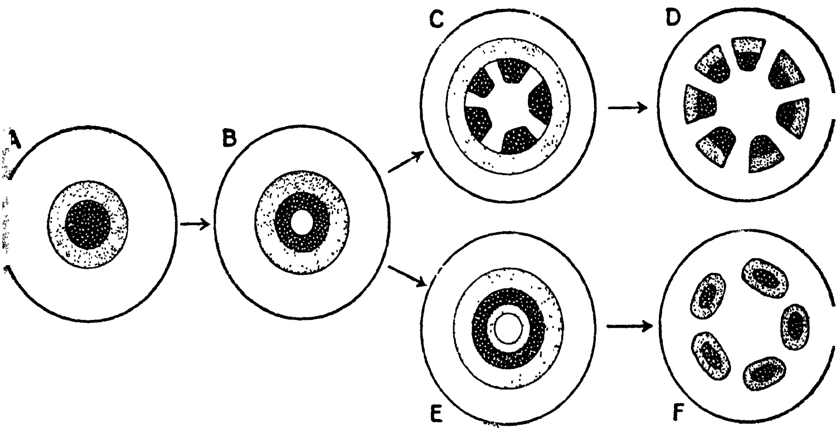

Fig. 119.—Diagrammatic figures of the types of vascular bundles. The pith and cortex are left white, the phloem shown by black dots, and the xylem by white dots on a black ground Explanation in the text.

of the STELAR THEORY (^{63}), the single central bundle is termed the STELE, and the circle of collateral or concentric bundles with the enclosed pith would also be regarded as a stele since it is derived from the primitive stele. A single bundle may therefore represent the whole stele or a part of the stele. There is usually only one stele or central cylinder in the stem of the Spermatophyta (monostely). Cases are, however, met with in which the stele is divided (polystely) as in the stems of *Auricula* and *Gunnera*.

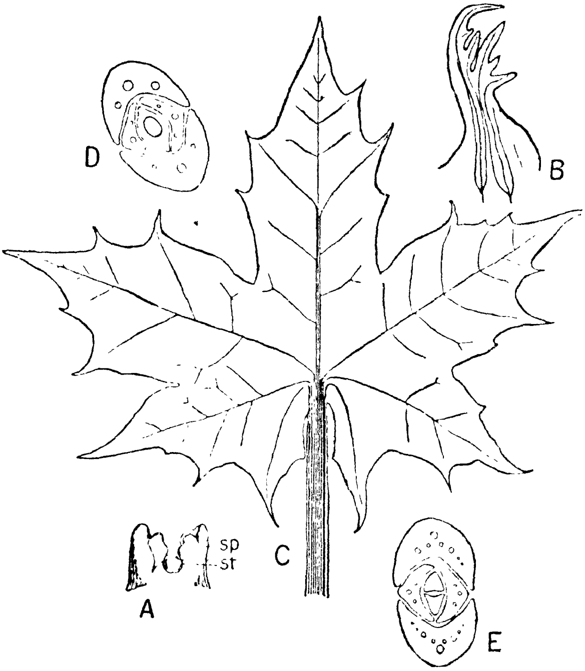

FIG. 120.—*Acer platanoides*. *A*, External view of a bud, with two young leaves between which the apical cone of the stem is visible; *sp*, the leaf-blade, in which five segments are indicated, the uppermost one being developed first; *st*, the zone, by the growth of which the leaf-stalk will arise later. *B*, An older leaf seen from the side; the young vascular bundles, which will later determine the venation, are indicated. *C*, Fully-grown leaf, with the course of the vascular bundles indicated diagrammatically. *D*, A transverse section of the basal portion of a bud showing three vascular bundles in each leaf. *E*, A similar section at a higher level; the number of vascular bundles has increased by branching. (After DEINEGA, from GOEBEL'S *Organography*. *A*, *B*, and *E* slightly magnified.)

(γ) The Leaves (^{64}). 1. Development of the Leaves.—The leaves have been seen to arise exogenously at the growing point of the stem as lateral papillae or bulges (Figs. 94, 98 *f*), which to begin with are unsegmented. These are the LEAF PRIMORDIA. Usually a young leaf occupies only a part of the circumference of the apex, but it may encircle the latter as an annular ridge. Several leaves forming a whorl may arise in the same way and only later appear as distinct structures on the ring-shaped outgrowth. When whorled leaves arise independently they may either appear simultaneously or, as is more commonly the case, in succession ([65]).

In rare cases a leaf may be terminal on the growing point.

While the shoot by means of its growing point has an unlimited growth, the growth of the leaf primordia, which only continues at their tips for a short time, is limited. The tip, which often develops more rapidly than the rest of the leaf, is first transformed into permanent tissue. This assists in the protection of the youngest parts of the bud, a function which has already been seen to be undertaken by the leaves. The further growth of the leaf is as a rule effected by intercalary growth. Most frequently the change into permanent tissue proceeds from the tip towards the base. The growth is thus greatest and most prolonged in the leaf-base, where it continues until the leaf is fully developed. Well-marked and prolonged apical growth is on the other hand characteristic of the leaves of many ferns.

Welwitschia mirabilis (cf. Fig. 630) behaves in a peculiar way unlike all other cormophytes. Above the cotyledons only a single pair of foliage leaves is formed. The basal zones of these grow in each annual period while the ends of the leaves are gradually withering.

2. Different Forms of Leaves.—The leaves of the shoot have very diverse functions and are correspondingly various in their form on the same stem, although in their origin they are alike.

The main axis of the seedling bears first the COTYLEDONS or seed-leaves which are situated on the hypocotyl (Fig. 152) of the embryo while it is yet in the seed. In the Monocotyledons there is only one such leaf, while the Dicotyledons and some Gymnosperms have two cotyledons and some Gymnosperms have more than two. Following on the cotyledons in the case of subterranean stems, and often also in those above ground, come a number of SCALE LEAVES (Fig. 121 *nd*), then in the case of aerial shoots the FOLIAGE LEAVES (*lb*), and still higher simply formed BRACTEAL LEAVES (*hb*). The foliage leaves may be first considered, since the other forms have arisen by transformation of these.

A. The Foliage Leaves exhibit a great variety of form and segmentation, and these characters are largely employed in descriptive botany. As a rule, the foliage leaf is segmented into the flattened, thin, bright-green LEAF-BLADE (lamina, Fig. 122 *sp*), which is often inaccurately spoken of as the leaf; the stem-like LEAF-STALK (petiole, Fig. 122 *s*); and frequently also into the STIPULES (*nb*) attached to the LEAF-BASE close to the stem or into a LEAF-SHEATH (vagina, Fig. 134 *v*) more or less completely surrounding the stem above the node. When the leaf-stalk is wanting the leaf is termed sessile; when present it is petiolate. The segmentation is recognisable at an early stage in the primordial leaves, which are differentiated shortly after their origin into the leaf-base (Fig. 123 *A* and *B*, *g*) and the upper leaf (Fig. 123 *A*, *B*, *o*). From the leaf-base the stipules (*g*) arise or it forms a leaf-sheath or a thickened pulvinus. Frequently it undergoes no special further development and is not distinguishable in the mature leaf. The leaf-blade (Fig. 120 *A*, *sp*) is developed from the upper leaf, and so also when this is present is the leaf-stalk (*A*, *st*). The latter develops relatively late by intercalary growth and is thus intercalated between the already present leaf-blade and leaf-base ; it is never inserted directly on the stem.

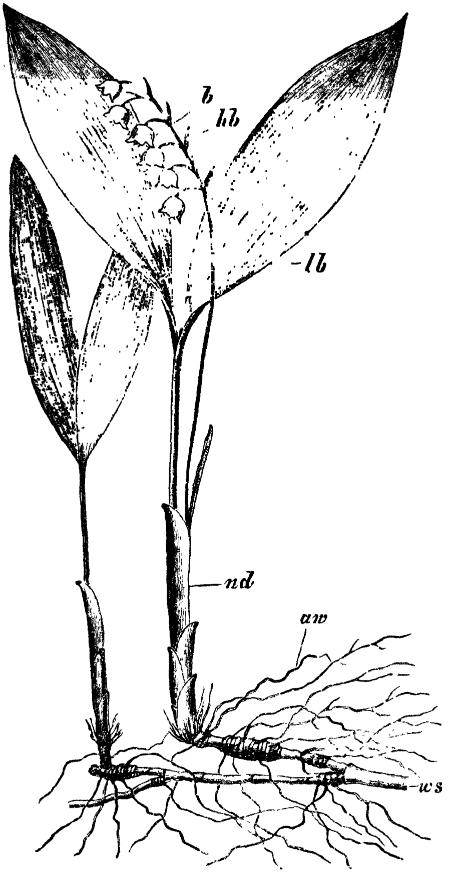

FIG. 121.—Lily of the Valley (*Convallaria majalis*). *nd*, Scale leaves ; *lb*, foliage leaves ; *hb*, bracts ; *b*, flower ; *ws*, rhizome ; *aw*, adventitious roots. (Somewhat reduced. After STRASBURGER.)

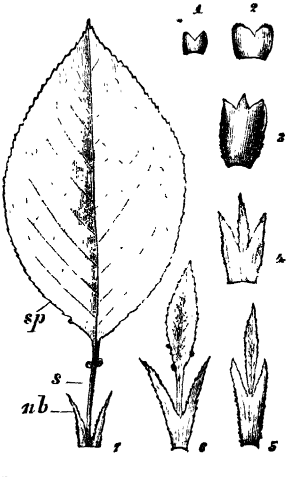

FIG. 122.—Bird Cherry (*Prunus avium*). Bud-scales (1-3) and the transition forms (4-6) to the foliage leaf (7) ; *sp*, leaf-blade ; *s*, leaf-stalk ; *nb*, stipules. (Reduced slightly. After SCHENCK.)

(a) The Leaf-blade. External Form (Fig. 124).—The leaf-blade which is as a rule definitely dorsiventral and of a deeper green colour on the upper side, may be entire or divided (Fig. 120 *C*), or composed of a number of leaflets. Such compound leaves arise by a process of branching from the margins of the primordia (Fig. 120 *A*). The leaves of Monocotyledons are usually simple, while compound leaves are common among Dicotyledons.

The margin of simple leaves (Figs. 121 *lb*, 122 *sp*) may be ENTIRE or slightly divided. If more deeply divided the leaf is described as LOBED when the divisions do not extend half-way to the middle of the leaf-blade, when they reach half-way as CLEFT, and when still deeper as PARTITE. The lamina is PALMATE (Fig. 138 *l*) or PINNATE (Fig. 136, 1-5), according to whether the divisions are directed towards the base of the leaf-blade or towards the midrib. Only when the separate divisions are so independent that they appear as distinct leaflets borne on a common petiole or on the original midrib is the leaf spoken of as COMPOUND (Fig. 136, 1-5); in all other cases it is termed SIMPLE. The leaflets of a compound leaf may be so segmented during their development as to resemble the main leaf, and in this way a leaf may be doubly or triply compound or more highly segmented. Simply pinnate or bi-pinnate leaves bearing leaflets on the two sides of the rachis of the first or second order are of frequent occurrence. In laminae, which become more or less branched during their development, the lateral divisions usually arise in basipetal order, *i.e.* proceeding from the tip towards the base (Fig. 120 *A*), but the opposite (acropetal) succession or a combination of the two is also met with.

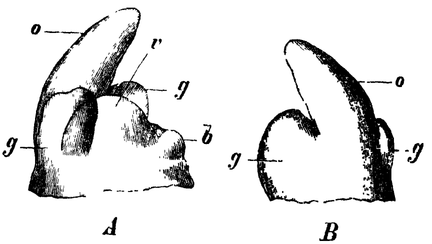

FIG. 123.—Development of the leaf in the Elm, *Ulmus campestris*. *A*, Showing the vegetative cone, *v*, with the rudiments of a young leaf, *b*, still unsegmented, and of the next older leaf, exhibiting segmentation into the laminar rudiment, *o*, and leaf-base, *g*. *B*, Showing the older leaf, viewed obliquely from behind. (× 58. After STRASBURGER.)

The lobed and frequently perforated leaf-blades of the Aroid, *Monstera*, originate by islands of tissue between the main veins dying and breaking down. The divisions of palmate and pinnate leaves of the Palms arise by a relatively late process of splitting within the originally entire, enlarging lamina. The direction of the dividing lines is determined by the folding of the young leaf-blade. Strips of tissue along the upper angles of the folds die, or their cell-walls become mucilaginous (*e.g.* in *Cocos* and *Chamaerops*) (65).

Sessile leaves usually clasp the stem by a broad base. Where, as in the case of the Poppy (*Papaver somniferum*), the leaf-base surrounds the stem, the leaves are described as AMPLEXICAUL.

The leaf-blade is traversed by green NERVES or VEINS which form a branched net-work. The thicker ribs project more or less from the surface on the lower side of the leaf, the upper surface often showing corresponding grooves. The finer veins become visible when the leaf-blade is viewed by transmitted light. Frequently the nerve in the middle line of the lamina is more strongly developed and is then termed the midrib; in other cases several equally developed main nerves are present. Lateral nerves spring from the one or more main nerves (Fig. 124).

The course of the nerves determines what is known as the VENATION of the leaf. The leaves of most Coniferae are UNI-NERVED. In leaves with more numerous veins, the DICHOTOMOUS VENATION must be distinguished as a special type which is characteristic of many Ferns and is also found in *Ginkgo biloba*; there is no midrib present in this case (Fig. 620). Most other leaves can be distinguished according to their venation as PARALLEL VEINED or NETTED VEINED. In parallel venation the veins or nerves run either approximately parallel with each other or in curves, converging at the base and apex of the leaf (Fig. 134 *s*); in netted veined leaves (Fig. 131) the veins branch off from one another, and gradually decrease in size until they form a fine anastomosing network. In leaves with parallel venation the parallel main nerves are usually united by weaker cross veins. Parallel venation is characteristic, in general, of the Monocotyledons; reticulate venation, of Dicotyledons and of some Ferns.

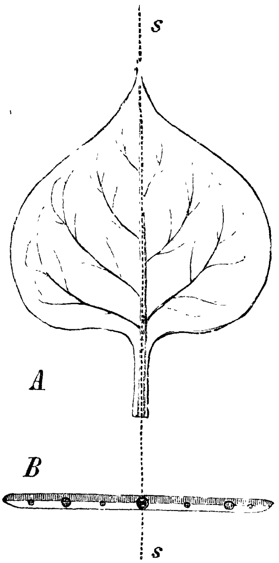

FIG. 124.—Diagram of a foliage leaf. *A*, Surface view. *B*, Transverse section; *s*, plane of symmetry. (After STRASBURGER.)

Internal Structure.—Foliage leaves exhibit considerable variety in structure, but are usually markedly dorsiventral (bifacial), the tissues towards the upper side being different from those below (Figs. 124, 125).

Many leaves, however, are similarly constructed above and below (equifacial, centric, Figs. 180, 186). This is the case especially in forms which grow in relatively dry situations, exposed to strong sunlight, but also occurs in submerged aquatic plants.

(*a*) EPIDERMIS.—The foliage leaf is bounded on all sides by a typical epidermis. In this, especially on the under side, there are numerous stomata, while on the upper side they are often absent (*e.g.* in almost all deciduous trees).

On the under side there are on the average 100-300 stomata to the square millimetre, but in some cases more than 700 may occur. Floating leaves tend to have stomata only on the upper surface.

The epidermis of the leaf may serve for water-storage and in such cases not uncommonly consists of several layers of cells.

(*b*) MESOPHYLL (^{66}).—The tissue of the leaf-blade between the upper and lower epidermis in the intervals between the ribs consists mainly of parenchyma and goes by the name of MESOPHYLL. The finer veins are embedded in it. Beneath the upper epidermis (Fig. 125 *ep*) come, as a rule, one to three layers of cylindrical parenchymatous cells elongated at right angles to the surface. These are called PALISADE CELLS (Fig. 125 *pl*; cf. 126 *A*), contain abundant chlorophyll, and have narrow, intercellular spaces between them. They constitute an assimilatory parenchyma. The cells often converge below in groups (Fig. 125) towards enlarged collecting cells (*s*).

In the leaves of many trees, *e.g.* the Copper Beech, differences in the thickness of the palisade layer are met with, its depth being much less in the "shade-leaves" than in the "sun-leaves." According to NORDHAUSEN's investigations(67), however,

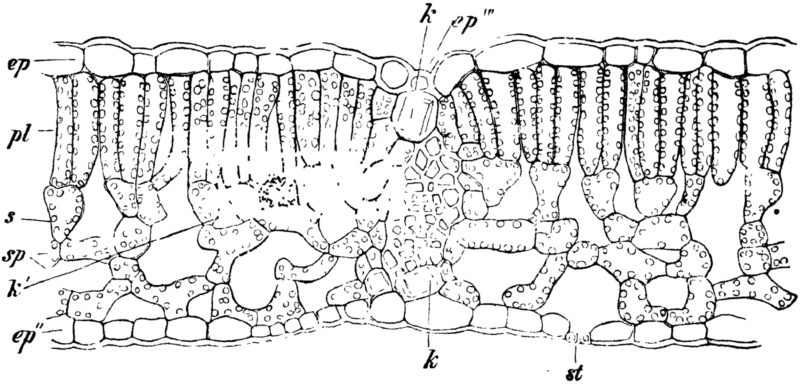

FIG. 125.—Transverse section of a leaf of *Fagus sylvatica*. *ep*, Epidermis of upper surface; *ep''*, epidermis of under surface; *ep'''*, elongated epidermal cell above a vascular bundle; *pl*, palisade parenchyma; *s*, collecting cells; *sp*, spongy parenchyma; *k*, idioblasts with crystals, in *k'* with crystal aggregate; *st*, stoma. (× 360. After STRASBURGER.)

no direct influence of the illumination exists. There are also plants (*e.g. Lactuca scariola*) which only form palisade cells in strongly illuminated leaves.

In some plants layers of cells placed parallel to the surface instead of at right angles to it are found in the usual situation of the palisade tissue. In the leaves

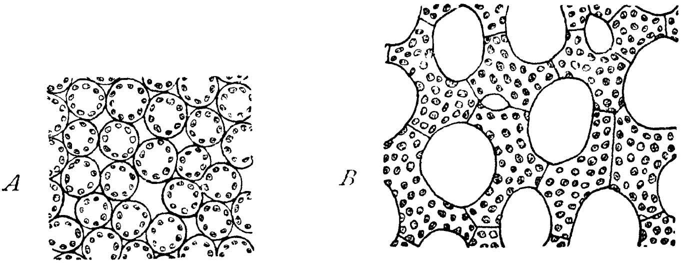

FIG. 126.—Tangential sections through the mesophyll of the foliage leaf of *Helleborus foetidus*. *A*, Palisade cells cut transversely. *B*, spongy parenchyma. (× 360.)

of the Pine and some other plants the same position is occupied by large, more or less isodiametric cells the internal surface of which is considerably increased by foldings of the cell walls (Fig. 127 *A*, *B fp*, *c*).

Below the palisade parenchyma comes what is known as the SPONGY PARENCHYMA (*sp*), which extends to the lower epidermis (*ep''*). The spongy parenchyma consists of irregularly-shaped cells with wide intercellular spaces and less chlorophyll than in the palisade tissue. The wide intercellular spaces stand in immediate relation to the stomata of the lower epidermis and serve for the transport of gases to the palisade cells.

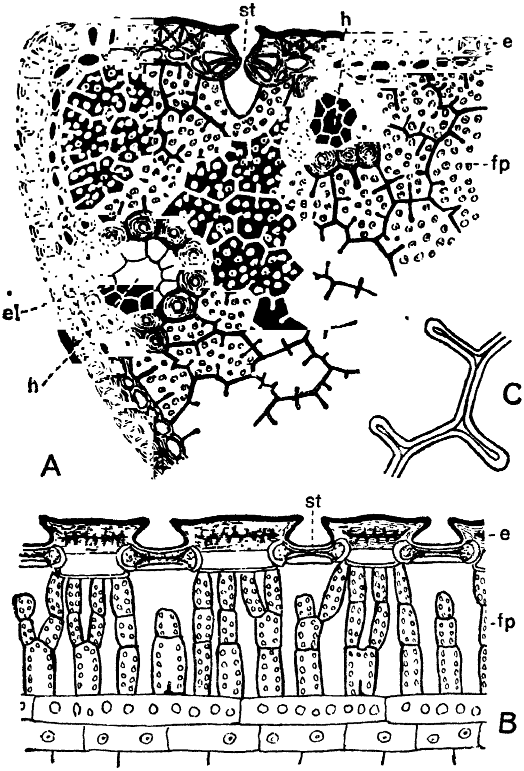

FIG. 127.—Leaf of *Pinus silvestris*. *A*, transverse section. *B*, median longitudinal section. (× 160.) *e*, epidermis; *st*, sunken stomata; *fp*, assimilatory parenchyma with infolded walls; *h*, resin canals, the thin-walled glandular epithelium (*el*) of which is surrounded by a sclerenchymatous sheath. *C*, portion of cell-wall from the assimilatory parenchyma. (× 380.)

HABERLANDT has estimated the number of chloroplasts per square millimetre of a leaf of *Ricinus* to be 403,200 in the palisade parenchyma and 92,000 in the spongy parenchyma. Thus in this case 82 per cent of the chloroplasts would belong to the upper and only 18 per cent to the lower side.

Colourless WATER-STORAGE TISSUE is frequently present in the mesophyll (Fig. 129 *W*).

(*c*) NERVES.—Within the nerves or veins one or more vascular bundles run. The abundant branching of these bundles to form a fine network is very characteristic of the leaf-blade and is shown clearly in leaf skeletons obtained by macerating leaves.

While the main nerves abut on the epidermis above and below, and interrupt the mesophyll, the finer veins are surrounded by mesophyll.

The structure of the vascular bundles in the lamina corresponds on the whole to that seen in the stem. In Phanerogams the bundles are usually collateral, and since they are continuations of the leaf-trace bundles from the stem the xylem is directed towards the upper, and the phloem towards the lower surface of the leaf.

As the bundles continue to ramify in the leaf-blade they become smaller and simpler in structure. The tracheae first disappear, and only spirally and reticulately thickened tracheides remain to provide for the water conduction. The phloem elements undergo a similar reduction. In Angiosperms, in which the sieve-tubes are accompanied by companion cells, the sieve-tubes become narrower, whilst the companion cells retain their original dimensions. Finally, in the cells forming the continuation of the sieve-tubes, the longitudinal division into sieve-tubes and companion cells does not take place, and TRANSITION CELLS are formed. With these the phloem terminates, although the vascular portion of the bundles still continues to be represented by short spiral tracheides. The ultimate branches of the bundles terminate blindly (Fig. 128).

The needles of Coniferae are usually traversed by 1-2 longitudinally-running bundles which do not exhibit branching. Along the outer margin of the xylem there is a development of peculiar, dead, tracheidal cells with bordered pits, while a corresponding development of cells rich in albuminous contents adjoins the phloem. This TRANSFUSION TISSUE, which may extend more or less into the living tissue of the leaf, facilitates the exchange of material between the nerves and the mesophyll.

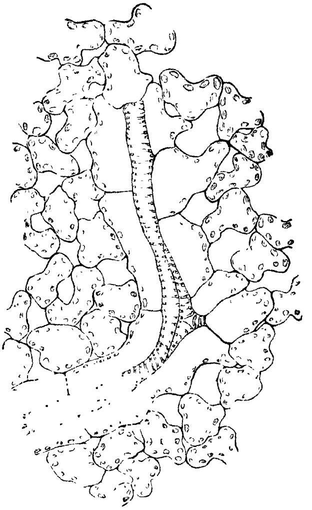
FIG. 128.—Termination of a vascular bundle in a leaf of *Impatiens parviflora*. (× 240. After SCHENCK.)

The bundles are surrounded by parenchymatous sheaths, which are composed of a number of layers of cells in the thicker nerves but of a single layer only in the finer branches. The cells of these sheaths are as a rule elongated and have no intercellular spaces. Strands of sclerenchymatous fibres are frequently present on one or both faces of the bundle (Fig. 129, 1), especially on the phloem side. Here, in the case of the larger bundles, the strand of sclerenchyma is curved; in cross-section it occupies the projection of the rib to the under side, and serves to give rigidity against bending to the lamina.

In some leaves strands of sclerenchyma also occur between the bundles (Fig. 129, 1) and also at the leaf margin. Such sclerenchymatous or collenchymatous strengthenings of the margin are protective against shearing forces that would tend to tear the lamina (Fig. 129, 2). Large leaf-blades which lack such marginal protection are torn by the wind (*e.g.* the Banana, Fig. 853).

EPITHEMA and WATER-STOMATA (68).—The mesophyll of the leaf-blade in certain families of Monocotyledons and Dicotyledons forms peculiar structures between the swollen ends of vascular bundles and the epidermis. They are composed of small living cells with colourless cell-sap, the intercellular spaces being filled with water. These masses of tissue go by the name of EPITHEMA and bring about the excretion of drops of liquid water. In this process their function is mainly passive, since they represent places where the resistance to filtration is least. The tracheides terminate in this epithema, and in the overlying epidermis there is a peculiarly-constructed stomatal apparatus in the form of WATER-

PORES (Fig. 130), which are of larger size than ordinary stomata. The guard-cells may be living and able to open and close the pore, but usually lose their living contents and the pore then remains permanently and widely open. The thickened ridges so characteristic of the guard-cells of ordinary stomata are usually lacking. The excreted liquid frequently contains calcium carbonate, which may remain as a white incrustation over the water-pores, as, for example, on the leaf margin in many species of *Saxifraga*.

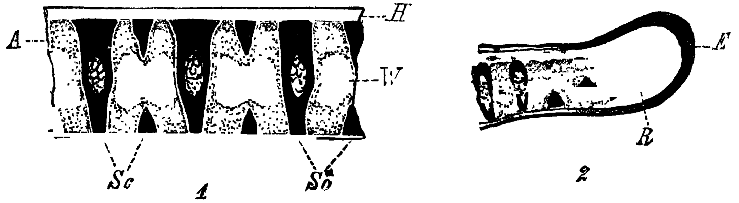

FIG. 129.—Leaf of *Phormium tenax*. 1. Transverse section; *Sc*, plates and strands of sclerenchyma; *A*, assimilatory parenchyma; *H*, epidermis; *W*, colourless water-storage tissue. 2. Edge of the same leaf; *E*, thick brown epidermis; *R*, marginal strand of sclerenchyma fibres. (After NOLL.)

At the tip of young leaves and of their marginal teeth such water-pores and epithemata frequently occur, but are dried up on the mature leaf. Water-pores also are found at the leaf-tips of submerged plants from which ordinary stomata are absent. They tend to perish early, breaking down with the adjoining tissue to leave open pits by which water and dissolved substances may be expressed.

From NECTARIES, either in flowers or on other parts of the plant, liquid containing sugar is excreted from special water-stomata.

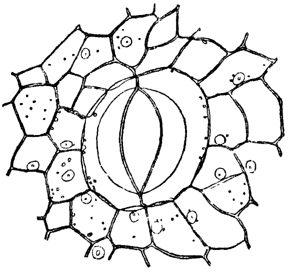

FIG. 130.—Water-pore from the margin of a leaf of *Tropaeolum majus*, with surrounding epidermal cells. (× 160. After STRASBURGER.)

Functions of the Leaf-blade.—The leaf-blades, as already mentioned, are the most important organs of nutrition, *i.e.* assimilation, and also of transpiration in cormophytes. Their form and structure, their arrangement, and the position they assume with regard to the direction of the light, correspond to this. Since the decomposition of carbon-dioxide is dependent both on light and on the presence of chlorophyll, the green colour of the lamina, the large surface exposed by it, its relative thinness and dorsiventral construction, are readily understood. The large surface enables a greater number of cells containing chlorophyll to be exposed to the light without shading one another; it also enables the carbon-dioxide to be obtained from the small proportion in the atmosphere, and at the same time facilitates the loss of water-vapour in transpiration. Since the passage of light through a few layers of cells filled with chlorophyll renders it ineffective for decomposing carbon-dioxide in the deeper layers, the assimilatory tissue is placed towards the upper surface of the leaf-blade. The carbon-dioxide is mainly taken into the leaf through the stomata of the lower surface. It can thus diffuse rapidly through the wide intercellular spaces of the spongy parenchyma, which is essentially a ventilating tissue, to the active assimilatory tissue of the upper side. This will take place more rapidly the thinner the leaf is.

The extensively-branched network of vascular bundles ensures the rapid passage of the products of assimilation from the assimilatory cells of every part of the leaf to the stem. At the same time it facilitates the most direct supply of water to all parts of the transpiring leaf-blade; the leaf-blade serves for giving off water, while the stem serves for conduction of water. Lastly, the venation increases the rigidity of the lamina.

It has been seen that the leaves are so arranged on the stem that the leaf-blades, which on erect shoots have a more or less horizontal position, are exposed to the light with the least shading by one another. Many leaves can place their blades at right angles to the incident light by their power of movement. In the case especially of dorsiventral, plagiotropous branches the leaf-blades seen from above are found to fit together more or less closely in a LEAF-MOSAIC, the upper surfaces of all being exposed to the light.

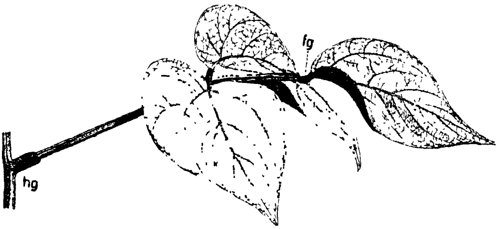

FIG. 131.—Imparipinnate leaf of *Phaseolus* with pulvini. *hg*, Main pulvinus at base of petiole; *fg*, pulvinus of one of the pinnae. (¼ nat. size.)

(b) **The Leaf-stalk** usually resembles a stem, and in its internal construction agrees with the midrib of the leaf-blade or sometimes with the stem. Typical assimilatory tissue is wanting, and the vascular bundles in the case of Angiosperms are usually arranged in an arc, open above. The leaf-stalk serves to carry the leaf-blade away from the stem and to place it suitably with respect to the light.

These movements of adjustment of the leaf to the light are sometimes carried out by special localised swellings at the base or the summit of the leaf-stalk, or in both situations. These LEAF-CUSHIONS or PULVINI work like hinges and occur in many Leguminosae (Fig. 131).

The leaf-mosaics formed by the current shoots of woody plants depend not only on movements of the leaves but on the various lengths of the petioles and the various sizes of the leaf-blades. The lower leaves have much longer stalks (and larger blades) than the upper ones. This is seen in the Sycamore and Horse-Chestnut and very beautifully in the floating rosettes of the Water Nut (*Trapa natans*).

(c) **The Leaf-base** (69).—When the leaf-base of a foliage leaf is specially formed, it usually serves to protect the bud and the younger leaves, enclosing the bud after the leaf-blade has unfolded.

STIPULES are frequently developed from the leaf-base; they stand one on either side of the leaf to which they belong, forming a pair (Fig. 123). They may be inconspicuous (Fig. 122 *nb*) or larger, and yellow or green in colour. When they serve only to protect the bud they are usually yellowish or brown, more simple in their structure than the leaf-blade, and are soon shed.

When the stipules take part in the assimilation of carbon-dioxide they are green and resemble the leaf-blade in structure (Fig. 202).

The arrangement of the stipules exhibits considerable variety. In many plants they occur as two free leaflets (Fig 122 *nb*). In others each stipule is united by one margin to the base of the petiole (sheathing stipules, Fig. 132 A); or they may be connected in various ways so as to form a tongue-shaped structure in the leaf-axil (axillary stipules, Fig 132 B) or so as to form a single structure on the opposite side of the stem from the leaf (opposed stipules). When the leaves are opposite the stipules may be united in pairs so as to give rise to interpetiolar stipules (Fig. 133). The stipules of a leaf may also surround the stem and form a closed tube which encloses the younger leaves of the bud. This is the case in the India Rubber plant (*Ficus elastica*) which is frequently grown in dwelling-houses; in this the sheaths are broken off at their bases and carried up on the next younger leaf as it unfolds. In the Polygonaceae they are broken through and remain as a dry sheath (OCHREA, Fig. 648) surrounding the stem.

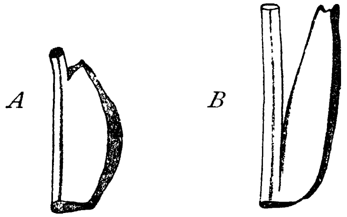

FIG. 132.—Stipules at the bases of petioles of the White Water Lily (*Nymphaea alba*). A, sheathing stipules; B, Axillary stipules. (After GLÜCK.)

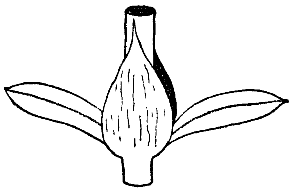

FIG. 133.—Node of *Paronychia argentea* (Cargophyllaceae). Right and left the leaves of a pair; in front and behind the interpetiolar stipules. (× 2½. After GLÜCK.)

In some species of *Galium* in which the stipules completely resemble the leaf-blades, there is an appearance of whorls of four, six, or eight leaves; in reality the arrangement of the two leaves is decussate, each leaf having one or more pairs of stipules according to the species. Only the two leaves have buds in their axils.

The leaf-base may form a SHEATH; this is more commonly the case in Monocotyledons than in Dicotyledons (*e.g.* Umbelliferae). In the Grasses (Fig. 134 *v*) the sheath is split along one side, but in the Cyperaceae it is closed. The sheath of the grass leaf, which encloses and supports the lower delicate portion of the still growing internode, continues at the base of the sessile lamina into a membranous outgrowth called the LIGULE (*l*); at its base immediately above the node the sheath is swollen (Fig. 134 *k*).

Heterophylly and Anisophylly.—Some plants bear diversely-formed foliage leaves either in different zones of the stem (HETEROPHYLLY, Fig. 135, 136) or in the same zone, but on the two sides of the shoot which thus becomes dorsiventral (ANISOPHYLLY, Fig. 137). Asymmetry of the leaves is often associated with anisophylly. Many water-plants exhibit heterophylly, having ribbon-shaped or highly-divided submerged water-leaves adapted to life in water and less divided stalked aerial leaves (Fig. 135). The leaves which the Ivy forms on the flowering shoots are essentially different in form from those which the plant has previously borne. This difference is even more marked in *Eucalyptus globulus*, which first bears oval sessile leaves and then sickle-shaped leaves. Not uncommonly the lowest leaves of the seedling (juvenile or primary leaves) are more simply formed than the later leaves.

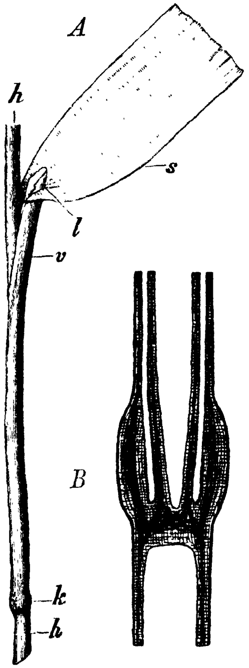

FIG. 134.—Part of stem and leaf of a grass. B. Node of grass in longitudinal section somewhat diagrammatic; *h*, Haulm; *v*, leaf-sheath; *k*, swelling of the leaf-sheath above the node; *s*, part of leaf-blade; *l*, ligule. (Nat. size. After SCHENCK.)

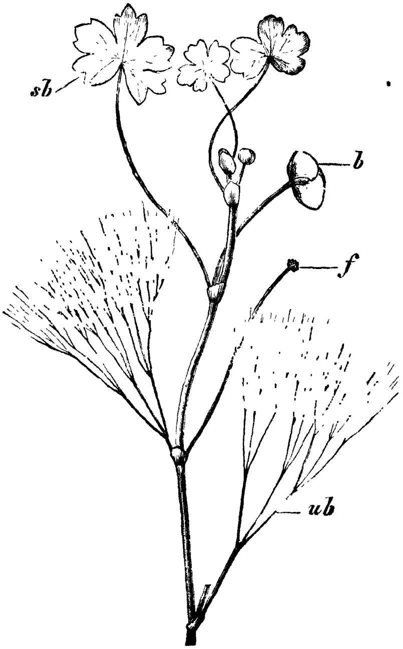

FIG. 135.—*Ranunculus aquatilis*. *ub*, Submerged leaves; *sb*, floating leaves; *b*, flower; *f*, fruit. (Reduced. After SCHENCK.)

B. The Seed-leaves or Cotyledons may be stalked or sessile, and are always more simple in form than the foliage leaves. They often, however, exhibit the same plan of segmentation.

The cotyledons may remain below the soil enclosed in the seed-coat (HYPOGEAL). In this case they are usually fleshy structures serving to store reserve food-material and are composed largely of storage-parenchyma. EPIGEAL cotyledons, which burst the seed-coat and appear above ground, tend to become green and then for a period assimilate carbon-dioxide like the foliage leaves.

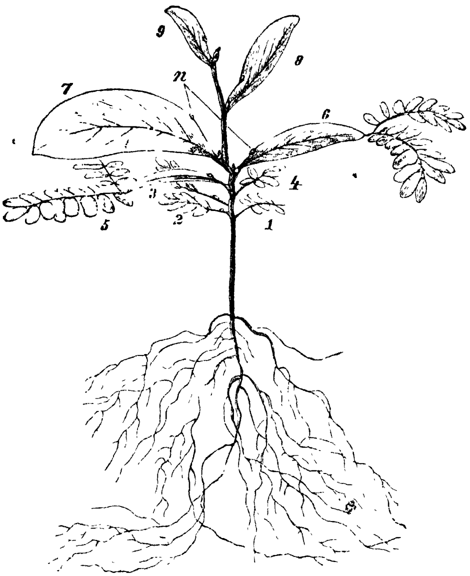

FIG. 136.—Seedling of *Acacia pycnantha*. The cotyledons have been thrown off. The foliage leaves *1-4* are pinnate, the following leaves bipinnate. The petioles of leaves *5* and *6* are vertically expanded; and in the following leaves, *7*, *8*, *9*, modified as phyllodes, bearing nectaries, *n*. (About ½ nat. size. After SCHENCK.)

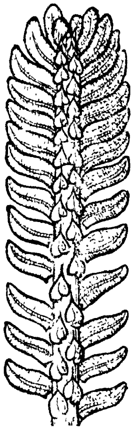

FIG. 137.—*Selaginella Martensii*. Anisophylly of the dorsiventral shoot. On the upper side of the stem are two rows of smaller asymmetrical green leaves and on either flank a row of larger asymmetrical leaves (slightly magnified).

C. The Scale-leaves and Bracteal Leaves, while indistinguishable from the foliage leaves in the early stages of development, are less differentiated than these when mature, being usually scale-like and sessile. They are developed by enlargement of the primordia, mainly from the leaf-base, while the lamina remains more or less undeveloped (Fig. 122 1-6, Fig. 138). Scale-leaves, either colourless or green, often occur on the aerial shoots before the foliage leaves (Fig. 121 *nd*). They are also the only foliar organs on rhizomes, appearing as hardly visible and usually short-lived scales, while, in accordance with the development in darkness, foliage leaves are wanting (Fig. 121 *ws*, Fig. 139). The bracteal leaves, on the other hand, resemble in construction the scale-leaves on aerial shoots, but are often variously coloured and tend to succeed the foliage leaves as the subtending leaves and bracts of the flowers or inflorescences. The internal structure of both scale-leaves and bracts is simpler than that of the foliage leaves. They hardly take part in the nutritive processes, but are usually protective structures for the young leaves or the buds. They are, however, connected with the foliage leaves by intermediate forms (Figs. 122, 138).

That scale-leaves and bracts are to be regarded as arrested forms of foliage leaves is shown not only by the developmental history but by the possibility of deriving foliage leaves from their rudiments or primordia. Thus Goebel succeeded in causing leaf-primordia that would have formed scale-leaves to become foliage leaves by removing the apex and stripping the leaves from the shoots. Subterranean stems, when forced to develop in the light, form foliage leaves from the primordia which in the earth would have become scale-leaves. In their internal structure, however, the scale-leaves and bracts are not merely arrested foliage leaves but frequently exhibit special differentiations connected with their particular functions (70).

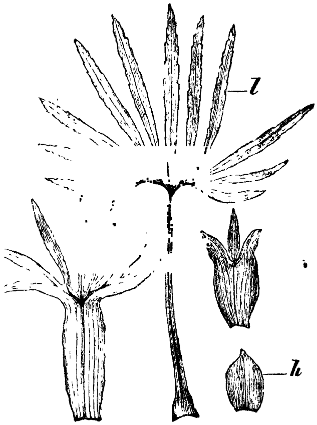

Fig. 138.—*Helleborus foetidus.* Foliage leaf (*l*) and intermediate forms between this and the bract (*h*). (Reduced. After Schenck.)

3. Duration of Life of Leaves.—In many plants the leaves have a shorter life than the stems on which they are borne. The leaves in such plants are shed from the stems (LEAF-FALL) or, in the case of subterranean shoots, decay while still attached. The leaves and stems of the aerial shoots of herbs die off together. LEAF-SCARS mark the places where the fallen leaves were attached to the stem. Plants in which the foliage leaves remain active for several seasons are called EVERGREEN in contrast to DECIDUOUS forms.

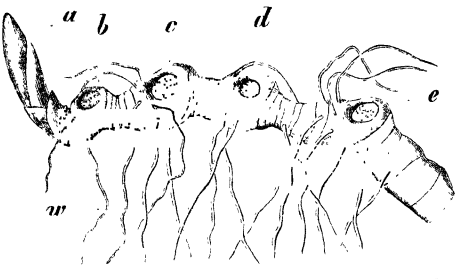

Fig. 139.—Rhizome of *Polygonatum multiflorum.* *a*, Bud of next year's aerial shoot; *b*, scar of this year's, and *c*, *d*, *e*, scars of three preceding years' aerial shoots; *w*, roots. (¾ nat. size. After Schenck.)

The fall of the leaves in phanerogamic woody plants is effected by means of a parenchymatous ABSCISS LAYER (71) which is formed at the base of the leaf-stalk shortly before the leaf is shed. In this region all the mechanical tissues of the petiole are greatly reduced, only the vessels being lignified. The separation of the leaf results from the rounding off of the cells of the absciss layer, the middle lamellae becoming mucilaginous, while the vessels and sieve-tubes are broken through.

The protection of the leaf-scar is effected by the cells exposed by the wound becoming transformed into a lignified cutis-tissue and, later, by the formation of a layer of cork produced from a cork-cambium and continuous with that covering the stem.

(δ) **The Branching of the Shoot** (58, 72).—The more foliage leaves that can be exposed to the sunlight on a shoot the greater will be the amount of organic substance formed by assimilation. In this respect, as will be evident, a branched system of shoots is greatly superior to a single erect shoot.

As in thalloid plants the branching of the shoot can happen in two ways. Rarely the shoot forks, dividing into two daughter-axes (DICHOTOMY). Usually the branching is LATERAL, the daughter-axes being thus formed on the main axis, which continues its growth.

A. Dichotomous Branching.—This is confined to the shoots of some Lycopodiaceae.

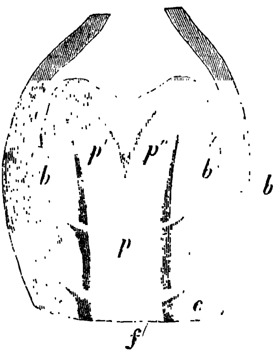

FIG. 140.—Longitudinal section of a bifurcating shoot (*p*) of *Lycopodium alpinum*, showing equal development of the rudimentary shoots, *p'*, *p''*; *b*, leaf-rudiments; *c*, cortex; *f*, vascular strands. (× 60. After HEGELMAIER.)

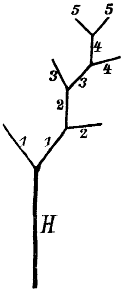

FIG. 141.—Sympodium arising from successive dichotomies.

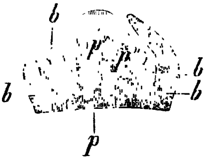

FIG. 142.—Bifurcating shoot (*p*) of *Lycopodium inundatum*, showing unequal development of the rudimentary shoots, *p'*, *p''*; *b*, leaf-rudiments. (× 40. After HEGELMAIER.)

In such Club-Mosses, when a shoot is about to divide into two equal branches, the circular outline of the growing point, in which no apical cell is recognisable, becomes elliptical. In the position of the foci of this ellipse the two new growing points project (Fig. 140). Not uncommonly in plants of this kind (*e.g.* in *Selaginella*) the branch-system deviates from the type described in that only one of the branches of each fork grows on further and again dichotomises (Fig. 141). If all the branches that in this way continue the branching are placed nearly in the same direction to which the other branches stand obliquely, the branch-system which results may readily be confused with racemose branching (Fig. 79 *b*). The main axis is, however, only apparently single, each portion being a daughter-axis of the portion that precedes it. Such an apparent axis is distinguished as a SYMPODIUM from a true main axis (MONOPODIUM), and the branching is sympodial and based on dichotomy.

All transitions from dichotomous to lateral branching are seen in the Lycopodiaceae. Some species form from the outset two growing points of unequal size, the smaller being soon displaced laterally in respect to the larger one (Fig. 142).

B. Lateral Branching. (a) Place of Origin of the Lateral Buds.—On shoots composed of axis and leaves the lateral branches as a rule occur on the axis or at the extreme base of the leaf. They are usually developed at the growing point of the parent-shoot in acropetal succession as exogenous outgrowths of the surface, in the same way as the leaf-primordia arise (Fig. 94 *g*). The positions in which the lateral shoots are developed are usually strictly determined. In Pteridophyta they frequently arise beside the leaf-primordia, but in Phanerogams, as a rule, where the upper side of the papilla forming the young leaf passes into the tissue of the growing point, *i.e.* in the LEAF AXIL. In some cases the branch is more on the leaf-base, in others it is distinctly on the main stem.

The primordium of a lateral branch may arise from the tissue of the axis close above the leaf-primordium and either after the origin of the latter (Fig. 143 *I*) or before the leaf has developed. In the latter case the leaf-rudiment arises from the tissue to the lower side of the branch-primordium (Fig. 143 *III*). On the other hand, the branch may be formed from the young leaf-primordium (Fig. 143 *II*).

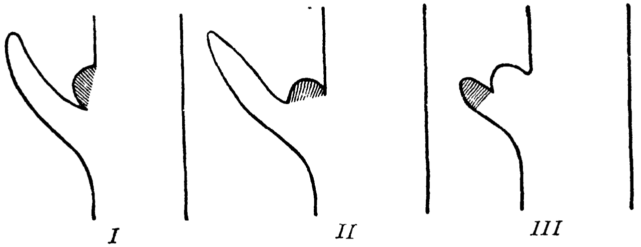

FIG. 143.—Diagrams of the developmental relations between the leaf-primordium and the axillary shoot. (After GOEBEL.)

In the longitudinal section of a growing point in Fig. 94 the youngest rudiment of a lateral shoot (*g*) is already visible, projecting in the axil of one of the uppermost leaves. In the axils of the following leaves the branch-primordia, since they arose in acropetal succession, are larger and have begun to form their leaves. The shoots developed from such AXILLARY BUDS are termed AXILLARY SHOOTS; the bud which terminates the growing end of the main shoot is termed, in contrast to the axillary buds, a TERMINAL BUD. The leaf, in the axil of which a bud stands, is its SUBTENDING LEAF (Fig. 145 *db*). The plane passing through the midrib of this leaf and the parent-axis is the MEDIAN PLANE of the leaf. Usually the axillary bud is situated in the median plane of its subtending leaf, but it may be displaced laterally. It is the rule in Angiosperms that each foliage leaf has an axillary bud; in some Gymnosperms, on the other hand, there is not an axillary bud to every leaf.

As a rule, only one bud develops in the axil of a leaf, but there are instances where it is followed by additional or ACCESSORY BUDS (73); these either stand over one another (serial buds), as in *Lonicera*, *Robinia*, *Gleditschia*, *Gymnocladus*, or side by side (collateral buds), as in many Liliaceae, *e.g.* species of *Allium* and *Muscari*.

A displacement from the position originally occupied by the members of a shoot frequently results from intercalary growth. A bud may thus, for example, become pushed out of the axil of its subtending leaf, and thus apparently have its origin higher on the stem (Fig. 144 *A*); or a subtending leaf in the course of its growth may carry its axillary bud along with it, so that the shoot which afterwards develops seems to spring directly from its subtending leaf (Fig. 144 *C*); or, finally, the subtending leaf may become attached to its axillary shoot, and, growing out with it, may thus appear to spring from it (Fig. 144 *B*).

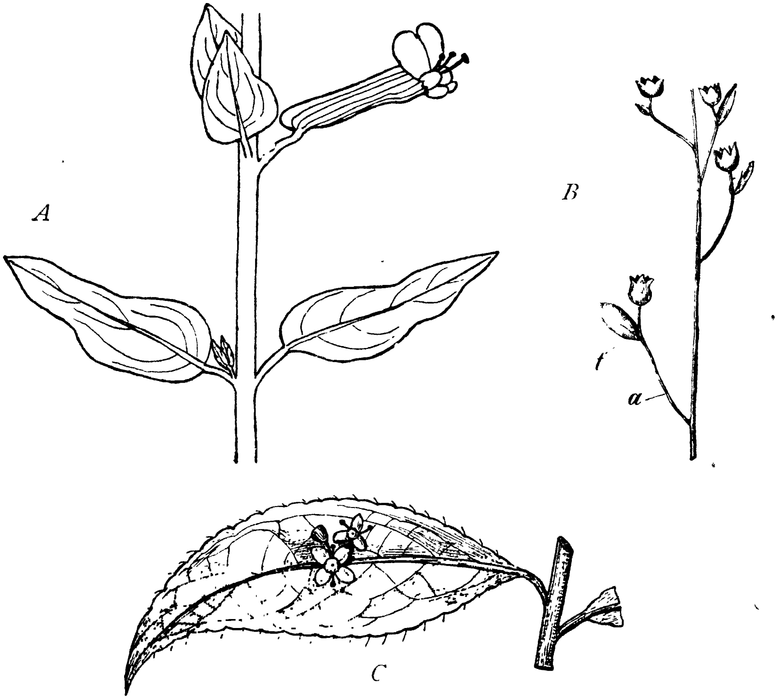

FIG. 144.—*A*, *Cuphea lanceolata* (Lythraceae), the vegetative axillary shoot in the axil of the lowest leaf on the left is not displaced; the shoot belonging to the lowest leaf on the right has formed a flower and is adherent to the stem to the level of the next pair of leaves. (½ nat. size.) *B*. *Samolus valerandi* (Primulaceae). The bract, *t*, is carried up on the axillary shoot, *a*, which ends in a fruit. (Nat. size. After SCHENCK.) *C*. Leaf of *Helwingia* (Cornaceae. East Asia.) The small male inflorescence is adherent to the foliage leaf to the middle of its lamina. (After SIEBOLD and ZUCCARINI.)

Shoots developing in predetermined positions on young parts of the plant are designated NORMAL, in contrast to ADVENTITIOUS SHOOTS, which are produced irregularly from the old or young portions of a plant, such as stems, roots, or leaves, and usually arise from permanent tissue which returns to the meristematic condition. Less commonly they develop from meristematic tissue persisting in their place of origin. Adventitious shoots, which arise from the older parts of stems or roots, are almost always ENDOGENOUS. They must penetrate the outer portions of their parent-shoot before becoming visible. Adventitious shoots formed on leaves, however, arise, like normal shoots, exogenously.

Such adventitious shoots frequently spring from the roots of herbaceous plants (*Convolvulus arvensis, Rumex acetosella*), or of bushes (*Rubus, Rosa, Corylus*), or of trees (*Populus, Ulmus, Robinia*). They may even develop from leaves, as in *Cardamine pratensis, Nasturtium officinale*, and a number of Ferns. An injury to a plant will frequently induce the formation of adventitious shoots, and they frequently arise from the cut surface of stumps of trees. Gardeners often make use of pieces of stems, rhizomes, or even leaves (Fig. 260) as cuttings from which to produce new plants (74).

(b) The Position of the Leaves of Lateral Buds.—When the relations of position

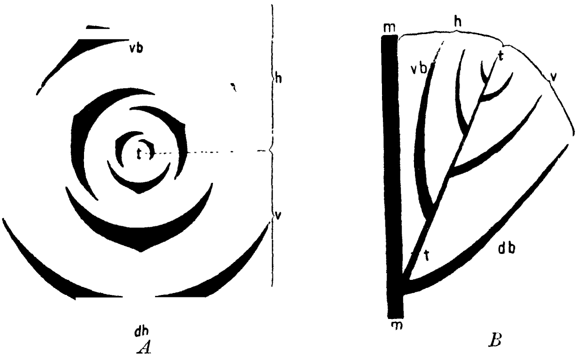

FIG. 145.—*A*, ground plan or diagram, and *B*, lateral view of a lateral bud of a Monocotyledon with a divergence of ½; *m*, parent-axis; *db*, subtending leaf borne on this; *t*, the daughter-axis; *vb*, bracteole on this; *h*, posterior, and *v*, anterior sides of the daughter-shoot.

in a lateral branch of any order are to be examined, the branch is placed with its subtending leaf (Fig. 145 *db*), towards the observer (ANTERIOR), and the parent-axis POSTERIOR (Fig. 145 *m*), and so that the median plane of the subtending leaf coincides with that of the observer. This median plane is then also the MEDIAN PLANE OF THE AXILLARY SHOOT (cf. Fig. 145 *t*). The plane at right angles to the median plane of the axillary shoot is then the TRANSVERSE plane of the latter (cf. Fig. 145 *A*). Structures on the lateral branch which lie between the transverse plane and the subtending leaf are termed ANTERIOR (*v*), while those lying between the transverse plane and the parent-axis are POSTERIOR (*h*). Right and left are applied to structures lying laterally with respect to the median plane. Median and transverse are applied to structures falling in these planes, while diagonal is used to refer to structures placed obliquely, *i.e.* between the median and transverse planes.

Independently of the phyllotaxis, the lowest leaves of a lateral bud which come next above the subtending leaf tend to occupy a definite position in relation to the latter and to the parent-axis. They connect the phyllotaxy of the lateral branch with that of the main shoot. In Monocotyledons there is one such BRACTEOLE

(Fig. 145 *vb*), while in Dicotyledons there are two bracteoles; they are usually scale or bracteal leaves. The bracteole in Monocotyledons is median and stands on the posterior side of the branch towards the main axis. It frequently has two lateral veins appearing as keels, while a middle vein is wanting (Fig. 145 *A*); it may thus be regarded as arising from the union of two lateral bracteoles (75). In Dicotyledons the two bracteoles (α and β) stand as a rule right and left in the transverse plane, the later leaves following in a different arrangement.

Apart from this the lateral buds may show the same leaf-arrangement as the parent-axis or may differ from this.

When the phyllotaxy is spiral the genetic spiral of the branch may either run in the same direction as that of the main axis (homodromous) or in the opposite direction (antidromous).

(c) Construction of the Branch System.—The general aspect or habit of every shoot-system depends, in addition to the direction of growth of its main axis, on the following features: the number of orders of lateral axes that develop; the position on the main axis of the buds which grow out as lateral branches; the intensity of the growth and the orientation of the lateral axes of various orders in relation to one another and to the parent-axis. The variety in the general habit of the shoot-systems frequently also stands in relation to the mode of life of the plants.

1. DIRECTION OF GROWTH OF THE MAIN AXIS OF THE SHOOT-SYSTEM.—This, in the first place, determines the general type of the shoot-system.

If the main axis stands at right angles to the soil, the shoot is termed ORTHOTROPOUS and the plant ERECT. In this case the more or less plagiotropous and dorsiventral lateral branches tend to be distributed radially when the plant is growing freely. If the main axis is growing obliquely or horizontally, and is thus PLAGIOTROPOUS, the arrangement of the branches is usually dorsiventral; when such a main axis with its lateral branches remains on the surface of the soil or grows horizontally beneath this, the plant is CREEPING. The lateral branches tend to come from the flanks and the roots from the lower surface of the main stem In such a plant, when lateral branches grow up at right angles to the soil, they behave as regards their further branching like erect plants.

2. THE ORDER OF SEQUENCE OF SHOOTS.—If the vegetative cone of the primary axis of a plant, after reaching maturity, is capable of reproduction, a plant with but one axis will result, and the plant is designated UNIAXIAL or HAPLOCAULESCENT. Usually, however, it is not until a plant has acquired axes of a second or third order, when it is said to be DIPLOCAULESCENT or TRIPLOCAULESCENT, or of the *n*th order, that the capacity for reproduction is attained. A good illustration of a plant with a single axis is afforded by the Poppy, in which the first shoot produced from the embryo terminates in a flower. As an example of a triplocaulescent plant may be cited the common Plantain (*Plantago major*), the primary axis of which produces only foliage and scale leaves; while the secondary axes give rise solely to bracteal leaves, from the axils of which finally spring the axes of the third order, which terminate in the flowers. In the case of trees, only shoots of the *n*th order can produce flowers. Thus a division of abour commonly occurs in a branched plant, which finds its expression in differences of form between the successive shoots. These differ in appearance

according to the special function performed by them, whether nutrition, storage, or reproduction. In addition to the essential members in the succession of shoots developed in a determined order, there are non-essential members which repeat forms of shoot already present. These may appear simultaneously with the essential shoots, and serve to increase the size of the plant, as in many annuals; in many perennial plants they arise as yearly innovations on the stock.

3. THE DISTRIBUTION OF UNFOLDING BUDS.—Only in relatively few cases, as, for example, in herbs, do all the lateral buds of a main axis proceed to grow on as shoots. As a rule many more lateral buds are formed than ever unfold. The remainder become DORMANT BUDS or perish. It would be a needless or even injurious expenditure of material on the part of the plant were all the buds to expand, since the branches would overshadow one another and some would perish.

Almost all trees possess, especially in the lower region of each annual growth, such dormant buds, which remain for a longer or shorter period capable of further development and can unfold under special conditions. The dormant buds of the Oak, Beech, etc., may be a hundred years old. The shoots that arise on old stems often come from these buds and are thus not adventitious.

The unfolding of lateral buds may proceed acropetally or basipetally, or exhibit no definite order. On highly-branched shoot-systems the more peripheral buds are favoured, since they have the best opportunity of favourable exposure of the leaves to the light.

Nearly all our native trees form only resting buds through the summer while the main shoots are elongating. Later, usually at the commencement of a new period of growth, some of the uppermost buds formed in the preceding season grow into lateral branches. These branches may form a whorl or an apparent whorl (*Araucaria, Pinus*); more commonly the highest buds form long shoots while those below them become short shoots (Pear, Apple).

4. DIRECTION AND INTENSITY OF GROWTH OF THE LATERAL BRANCHES IN RELATION TO ONE ANOTHER.—The lateral angle between adjacent lateral branches on an orthotropous branch may be very constant in any kind of plant (*e.g.* in *Araucaria* or *Pinus*).

On the other hand, the intensity of growth of the lateral axes on the same main axis may show much variety. Frequently, with the appearance of a division of labour, only some of the branches are of unlimited growth, the others forming short shoots. The latter have usually a shorter life, tend not to branch, and do not take part in the persistent branch-system of the tree. In the Larch (Fig. 628), for example, the short shoots form short rosettes of needles on the older shoots of unlimited growth; cf. also the Pine (Fig. 627).

5. DIRECTION AND INTENSITY OF GROWTH OF THE LATERAL BRANCHES IN RELATION TO THE MAIN AXIS. DIFFERENT TYPES OF LATERAL BRANCHING.—The angle at which the lateral branch is inclined to its main axis also tends to be very constant in any species. It is usually less than 90°, rarely greater.

The lateral branches may grow at the same rate as the parent-axis, or less rapidly, or much more rapidly. In the last case they take precedence of the main axis, the growth of which may cease entirely, while one or more lateral branches take over the continuance of the branching. Diversity in the resulting branch-systems must evidently result from such differences in the growth of the daughter- and parent-axes. This has led to the distinction of various types of lateral branching, a knowledge of which is indispensable to the understanding of the morphological construction of the higher plants. The differences are especially well seen in the INFLORESCENCES of the flowering plants (cf. Special Part). It is characteristic of many inflorescences that the axillary buds of all the bracts are developed further. Owing to this the inflorescences, in contrast to the vegetative shoot-systems, form crowded branch-systems.

(*a*) The term **racemose branching** is applied when the main axis grows MORE ACTIVELY than the lateral axes of the first order, and these in turn more actively than the branches of the second order arising on them; also when the main axis grows as actively as its daughter axes. In the former case a true main axis or MONOPODIUM can be followed throughout the entire branch-system (cf. Fig. 79 *b*). Such typical MONOPODIAL BRANCHING is exhibited, for example, by the Pine and other Conifers with a pyramidal outline; the radial orthotropous main shoot grows vertically upwards under the influence of gravity (cf. p. 341), while the dorsiventral lateral branches of the first order diverge on all sides horizontally from the main axis. If the lateral branches of the first order grow erect, as in the Cypress and in many shrubs, there may be no difference in length between them and the main axis; the branch-system has in such cases an oval or spherical form.

(*b*) The term **cymose branching** is applied when the main axis grows LESS STRONGLY than the lateral axes, which continue the branching and in their turn are overtopped by the branches they bear. The resulting appearance differs according to whether several, equally strong, lateral axes of the same order, or only one lateral axis, continue the branch-system. In the latter case an apparent main axis or SYMPODIUM is formed.

In many cases of cymose branching the parent-axis not merely grows more slowly than the daughter-axes but its tip dies or is cast off. This happens in many of our trees such as the Willow or the Lime.

I. If more than two lateral branches of the same order continue the branching the term PLEIOCHASIUM is used. Such lateral branches are usually approximated to the upper end of the parent axis and radiate on all sides obliquely upwards, in some cases being arranged in a whorl. The inflorescence of *Euphorbia* affords an example.

II. If two lateral branches of the same order continue the branching and stand opposite to one another, forming an acute or right angle,' the term DICHASIUM is used. This is shown diagrammatically in Fig. 146, with which the dichasial inflorescence in Fig. 558 may be compared. A branch system of this kind, another example of which is afforded by the Mistletoe, which grows parasitically on trees, simulates a dichotomy (Fig. 652). The successive pairs of lateral branches do not lie in one plane as in the diagram but stand at right angles to one another so that they diverge on all sides. Only a ground plan (Fig. 148 *E*) can therefore represent the true arrangement of the members of the branch-system.

III. When the branching is continued by a single lateral branch the term MONOCHASIUM is used. Frequently this branch continues the direction of the parent-shoot, the tip of which is displaced to one side (Fig. 147). In this way a branch-system with a sympodial axis composed of lateral members of successive orders is formed, as was seen to be the case sometimes in dichotomous branching (p. 116). Such a branch-system may closely resemble monopodial branching, especially when, as is frequently the case, the sympodium stands vertically and the arrested ends of the branches appear as if borne laterally upon it. They are distinguishable from truly lateral branches, however, by the regular absence of a subtending leaf, while a leaf which stands opposite to each apparent branch is really the subtending leaf of the daughter-shoot that continued the sympodium (cf. Fig. 147). The further branching may also be sympodial. The branching of many trees, such as the Lime and Beech, is of this nature, but the sympodial construction is not recognisable in the stems and branches. It remains evident, however, in many subterranean shoots such as the rhizome of *Polygonatum multiflorum* (Fig. 139). The terminal bud of each year's growth becomes the aerial shoot, while an axillary bud continues the growth of the rhizome in the soil.

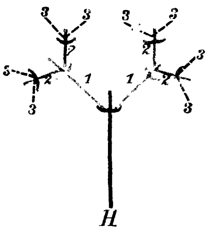

FIG. 146.—Diagram of the Dichasium. *H*, Axis of the seedling; *1*, *2*, *3*, daughter-axes of the corresponding first, second, and third orders.

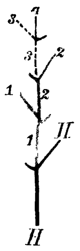

FIG. 147.—Diagram of the Monochasium. Cf. Fig. 148.

According to the relation of the lateral shoots of different orders to each other there arise monochasial branch-systems of diverse and very characteristic construction. The branching frequently proceeds from the axil of a bracteole.

A. The median plane of all the lateral shoots may coincide with the median plane of the lateral shoot of the first order.

(*a*) The successive lateral branches are on the anterior side of the parent-axis, *i.e.* between the latter and the subtending leaf (cf. p. 119). In lateral view they thus fall on the same side, DREPANIUM (Fig. 148 *C*, *D*).

(*β*) The successive axes stand on the posterior side of the parent-axis (cf. p. 119) and in lateral view appear alternately right and left, RHIPIDIUM (Fig. 148 *A*, *B*).

B. The median plane of each lateral shoot (of the 1st, 2nd, 3rd order, etc.) is always transverse, *i.e.* right or left of the median plane of the subtending leaf on the parent-shoot. Such branch-systems can only be represented in ground plan.

(*a*) The successive lateral shoots are placed always to the same side, either to the right or the left, BOSTRYX (Fig. 148 *F*).

(*β*) The successive lateral shoots stand alternately to the right or left, CINCINNUS (Fig. 148 *G*).

The bostryx and cincinnus are readily understood by deriving them from the ground plan of the dichasium (Fig. 148 *E*).

Various types of branching are frequently combined in one branch-system. Thus cymosely-branched lateral shoots may be borne on the racemose main shoot. The combinations are especially varied in the case of inflorescences (cf. the Special Part).

(b) The Root (76)

The ROOTS of plants, which are usually situated in the soil (subterranean roots) and less commonly exposed to the atmosphere (aerial roots), NEVER BEAR LEAVES. In this respect, as well as by the absence of the green colour, their appearance differs from that of shoots; even of colourless subterranean shoots. Their chief functions are to attach the plant to the soil and to absorb from this water and salts that are conducted to the shoot-system. The functions of roots are thus very different from those of most shoots.

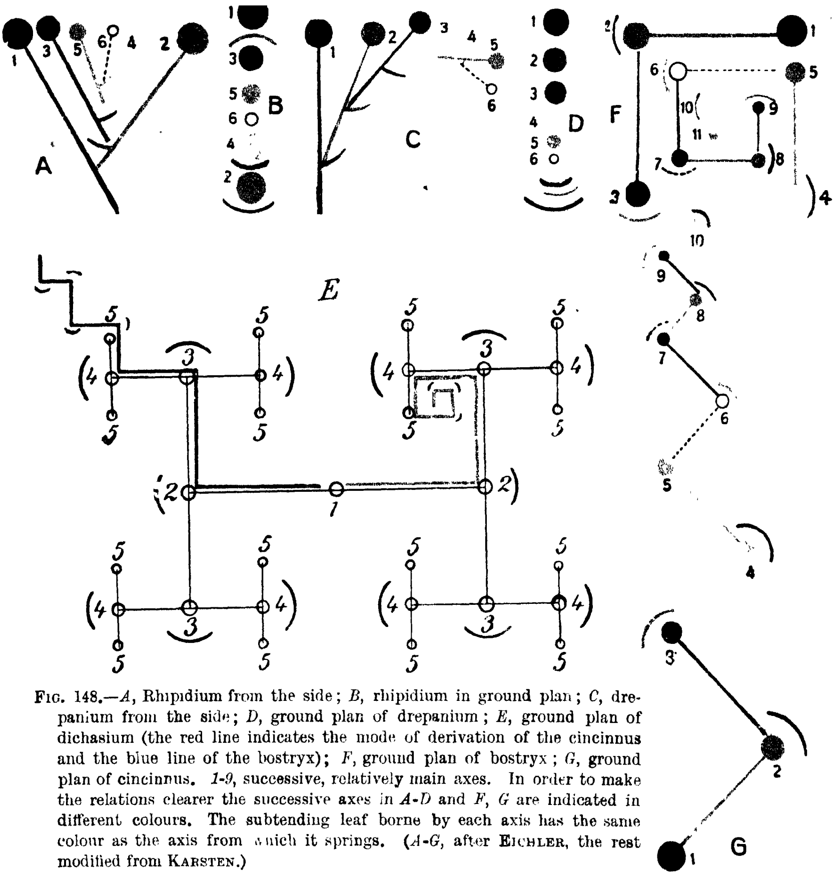

FIG. 148.—*A*, Rhipidium from the side; *B*, rhipidium in ground plan; *C*, drepanium from the side; *D*, ground plan of drepanium; *E*, ground plan of dichasium (the red line indicates the mode of derivation of the cincinnus and the blue line of the bostryx); *F*, ground plan of bostryx; *G*, ground plan of cincinnus. *1-9*, successive, relatively main axes. In order to make the relations clearer the successive axes in *A-D* and *F*, *G* are indicated in different colours. The subtending leaf borne by each axis has the same colour as the axis from which it springs. (*A-G*, after EICHLER, the rest modified from KARSTEN.)

1. Growing Point.—The root grows in length at the tip, exhibiting APICAL GROWTH by means of its conical GROWING POINT. The latter requires to have the thin-walled meristematic cells specially protected, since, as the root grows, it is forced forwards like a needle between the angular particles of the soil. This protection is afforded by a special organ composed of permanent tissue which is called the ROOT-CAP or CALYPTRA; it covers the tip of the root as a thimble does that of the finger, the true growing point having an intercalary position within the tissue of the root-tip. The outer cell-walls of the root-cap become mucilaginous, and this makes the forward passage of the root easier. The root-cap is usually only recognisable in median longitudinal sections through the root-tip (Figs. 149, 150), but in some cases (*Pandanus*) the cap is to be clearly seen on the intact root.

The very noticeable caps on the water-roots of Duckweed (*Lemna*) and of some Hydrocharitaceae are not really root-caps, as they are not derived from the root, but from a sheath which envelops the rudimentary root at the time of its origin. They are accordingly termed ROOT-POCKETS. The root-pocket performs all the functions of a root-cap.

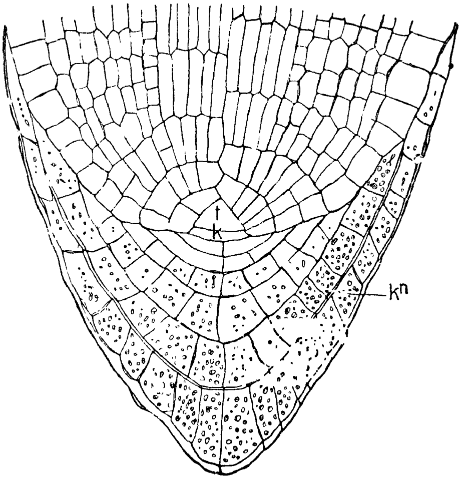

FIG. 149.—Median longitudinal section of the apex of a root of the Fern, *Pteridium creticum*. *t*, Apical cell; *k*, initial cell of root-cap: k^n, root-cap. (× 160. After STRASBURGER.)

In resting periods, when the growth of subterranean roots has ceased, the parenchymatous cells of the root-cap may become corky or converted into a cutis tissue which further encloses and protects the root-apex (77).

The growing point of the root is composed of meristematic cells from which the permanent cells of the root-cap are derived on the side towards the tip and the permanent tissue of the root on the basal side.

In most Pteridophytes the root, like the shoot, has a three-sided apical cell (*t*, Fig. 149) with the form of a three-sided pyramid. In addition to the segments cut off parallel to the three inner walls which contribute to the root itself, segments are formed parallel to the outer wall (*k*). These undergo further divisions and form the root-cap.

The growing points of the roots of Phanerogams, on the other hand, have no apical cells. They consist of equivalent meristematic cells that are frequently arranged in regular layers. The apex of a root of one of the Gramineae (Fig. 150) may be described as an example. The stratified meristem, from which the permanent tissue of the root arises, is separated into an outer layer of cells, the DERMATOGEN (*d*) ; a central region formed of several layers which gives rise to the central cylinder of the root and is called the PLEROME (*pl*) ; and into a number of layers between the dermatogen and plerome which form the PERIBLEM. The dermatogen (*d*) and periblem (*pr*) unite at the apex in a single cell-layer, outside of which lies the CALYPTROGEN (*k*) or layer of cells from which the root-cap takes its origin.

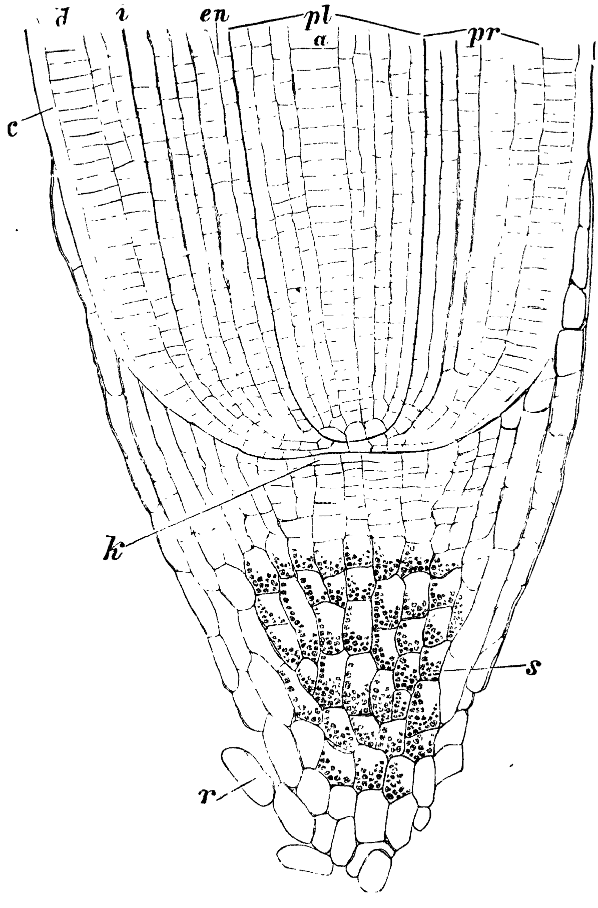

FIG. 150.—Median longitudinal section of the apex of a root of the Barley, *Hordeum vulgare*. *k*, Calyptrogen; *d*, dermatogen; *c*, its thickened wall; *pr*, periblem; *pl*, plerome; *en*, endodermis; *i*, intercellular air-space in process of formation; *a*, cell-row destined to form a vessel; *r*, exfoliated cells of the root-cap; *s*, large, moveable, starch grains in the cells of the root-cap. (× 180. After STRASBURGER and KOERNICKE—modified.)

In many other roots, however (in the majority of Dicotyledons), the formation of the root-cap results from the periclinal division of the dermatogen itself, which, in that case, remains distinct from the periblem. In Gymnosperms, and in many Leguminosae, the dermatogen, periblem, and calyptrogen are not marked out as distinct regions.

2. External Features of the Root.—Behind the growing point the meristematic cells enlarge greatly as they are transformed into permanent tissue, a marked elongation of the root accompanying these processes. By this growth in length, which begins close behind the apex and in subterranean roots is limited to a zone only 5-10 mm. long, the root becomes a cylindrical colourless structure.

The zone of elongation in aerial roots may be many centimetres in length. Its shortness in subterranean roots is evidently connected with the conditions of their life.

At some distance from the root-tip, about the region where growth in length ceases, the ROOT-HAIRS ([78]) (Fig. 151, Fig. 152 r), which are important appendages of subterranean roots, appear. They are localised tubular protrusions of the living epidermal cells with thin walls covered with mucilage. When seedlings, *e.g.*, of Wheat are grown in a moist chamber they can be seen with the naked eye, forming a delicate down on the surface of the root. They occur in enormous numbers (*e.g.* about 420 per sq. mm. in *Zea Mays*). Their length varies, according to the kind of plant, between 0·15 and 8 mm. They enlarge the surface of the root greatly (in *Pisum*, for example, twelvefold) and penetrate between the particles of the soil and become attached to them. Thus in the soil they do not retain the cylindrical form seen in moist air but are bent to and fro, and flattened, club-shaped, or lobed at the top (Fig. 234). They serve to absorb water and dissolved salts. They only live for a few days, the older root-hairs dying off as new ones form nearer the tip; thus only a limited zone of the young root some centimetres or millimetres in length is clothed with them. The older smooth portion of the root serves for conduction, but has ceased to absorb the water. The surface often shows transverse wrinkling brought about by subsequent contraction of this region of

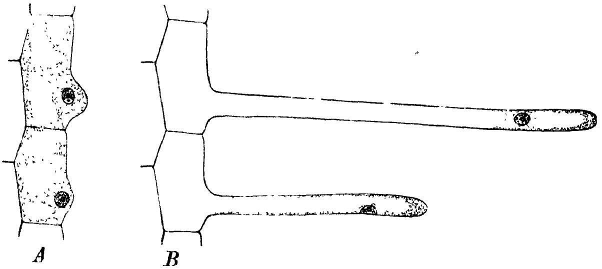

FIG. 151.—Epidermis of the root in longitudinal section showing root-hairs (*B*) and their origin (*A*). (After ROTHERT, semi-diagrammatic.)

the root. This shortens the root so that, like a tense support, it anchors the shoot more firmly in the soil (cf. Fig. 200, 6).

Root-hairs are wanting in some plants, especially those which can readily obtain water, as is the case with many aquatic and marsh plants. The roots of some aquatic plants, such as *Nuphar luteum*, form root-hairs when they penetrate the soil ; the roots of marsh plants, such as *Carex paludosa*, when there is lack of water.

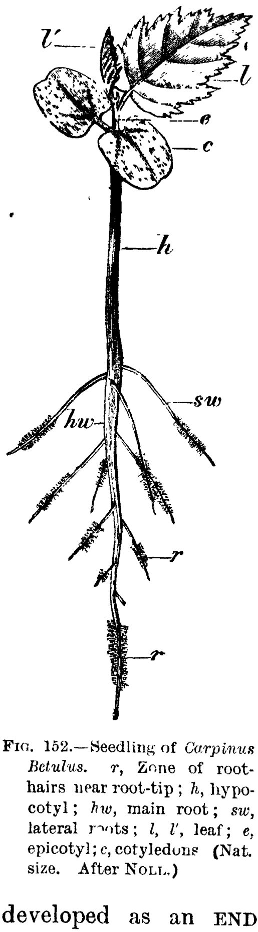

FIG. 152.—Seedling of *Carpinus Betulus*. *r*, Zone of root-hairs near root-tip ; *h*, hypocotyl ; *hw*, main root ; *sw*, lateral roots ; *l*, *l'*, leaf ; *e*, epicotyl ; *c*, cotyledons (Nat. size. After NOLL.)

3. Primary Structure of the Root.—When the transformation of the meristematic cells into permanent tissue has taken place the same kinds of tissue are recognisable in roots as in shoots, their arrangement being as a rule radially symmetrical. The surface of the younger portions of the root is bounded by the thin-walled EPIDERMIS which, with the root-hairs borne upon it, serves for absorption. The ABSENCE OF STOMATA and of a CUTICLE is characteristic of this layer. The epidermis of the root dies off with the root-hairs. The outermost layer of the cortex then forms a cutis-tissue called the EXODERMIS (79) on the surface, the cell-walls becoming more or less suberised (Fig. 153 *ex*).

Some of the cells of the exodermis often remain unsuberised and serve as transfusion cells. They are regularly placed among the corky cells and smaller than the latter.

The remaining tissues of the root can be distinguished into cortex and central cylinder.

The primary CORTEX of subterranean roots is composed of colourless tissue, which is usually parenchymatous. In the outer layers the cells are in close contact with one another, but intercellular spaces are present more internally. In the cortex of aerial roots, on the other hand, chlorophyll is present. The innermost layer of the cortex is usually developed as an ENDODERMIS (80) (Figs. 153 *e*, 154 *S*, 156 *s*), which sharply marks the limit between cortex and central cylinder.

Owing to the presence of the Casparyan strips on the radial walls of the epidermal cells (cf. p. 54), the central cylinder is to a certain extent shut off from the primary cortex ; the tangential walls of the young endodermal cells, however, allow of passage of water between the two regions. In the older parts of the roots the cells of the endodermis become corky, and in many Monocotyledons are greatly thickened, but generally on one side only. Should thickening occur at an early stage, special endodermal cells, directly external to the xylem-strands, remain unthickened and serve as TRANSFUSION CELLS (Fig. 156 *d*).

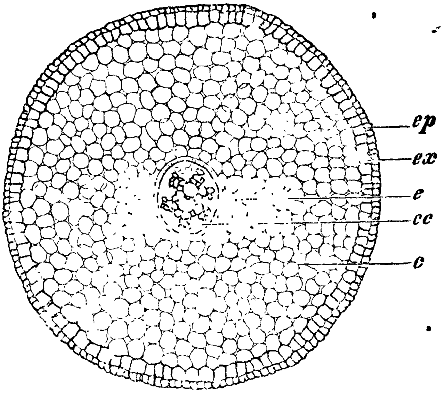

FIG. 153.—Transverse section of an adventitious root of *Allium Cepa*. *ep*, Remains of the epidermis; *ex*, exodermis; *c*, primary cortex; *e*, endodermis; *cc*, central cylinder. (× 45. After M. KOERNICKE.)

The outermost layer of cells of the central cylinder lying immediately within the endodermis (Figs. 154 *pc*, 156 *p*) forms the PERICYCLE; this is usually a single layer and in rare cases is wanting. The strands of xylem and phloem run longitudinally in the central cylinder and in all roots form a radial vascular bundle ([33]) (cf. p. 95). Roots are described as diarch, triarch, polyarch, etc., according to the number of the vascular strands. Thus the root in Fig. 154 is tetrarch and that in Fig. 156 pentarch.

The vascular strands may either meet in the centre (Figs. 154, 156) or there is in this position a central strand composed of parenchyma or sclerenchyma or a mixture of these tissues (Fig. 158).

Most roots have to be constructed to resist pulling strains, and the mechanical tissue is accordingly mainly placed compactly in the central region (Fig. 155). For an organ that has to resist tension it is immaterial at what part of the cross-section the mechanical tissues are placed. Their association in the centre to form a single strand is of advantage, however, since, if many thinner strands were situated peripherally, a one-sided pull might rupture some of these more readily. Sometimes mechanical tissues are also present in the cortex, (Fig. 155 *2*) and in such cases the roots are also rigid against bending and compression.

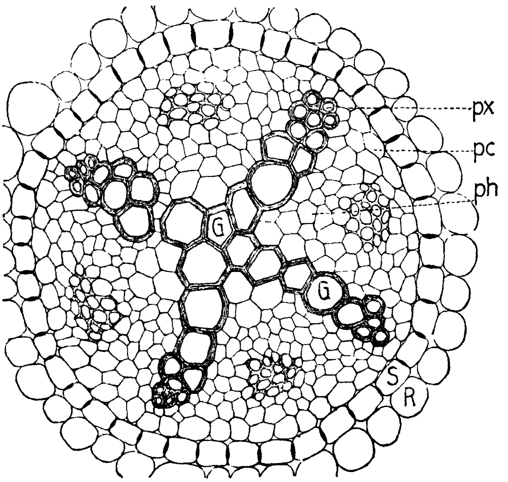

FIG. 154.—Transverse section of the radial bundle of the root of *Ranunculus acer*. *R*, Cortical parenchyma; *S*, endodermis; *pc*, pericycle; *ph*, phloem; *px*, protoxylem; *G*, xylem. (× 160 ROTHERT modified from DIPPEL.)

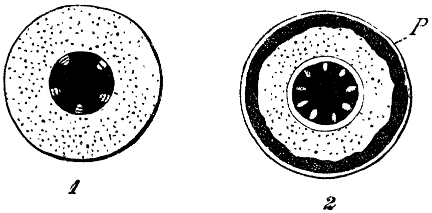

Fig. 155.—Mechanical tissue of roots. 1, Centrally placed to resist longitudinal pulling strains; 2, a prop root with a peripheral layer of mechanical tissue (*P*) to resist lateral pressure, in addition to the central strand. (After Noll.)

The continuity of the xylem- and phloem-strands of the radial bundle of the root with the corresponding tissues of the differently-constructed bundles of the stem (81) is effected at the junction of the root and stem of the seedling. It need only be briefly described for the most common case of plants in which the bundles of the stem are collateral (cf. Fig. 157). The essential fact of the transition is that each of the strands of xylem of the root rotates through 180° round its longitudinal axis. According to Chauveaud the protoxylem strands do not take part in this movement, but are absorbed. A number of collateral vascular bundles are reconstituted from the tissues of the radial bundle of the root by the radially-arranged xylem and phloem taking up the collateral position. This happens in different ways, of which two main types may, according to Van Tieghem, be distinguished: 1. The strands of xylem when rotating follow a straight course from the root to the stem; the strands of phloem of the root, on the other hand, divide radially, the two halves separate tangentially, and, uniting with the portions derived from adjoining strands of phloem, come to lie outside the xylem-strands (Fig. 157, A). 2. The phloem-strands of the root follow a straight course into the stem, but the strands of xylem which rotate through 180° split radially; the halves separate tangentially (as the phloem-strands did in

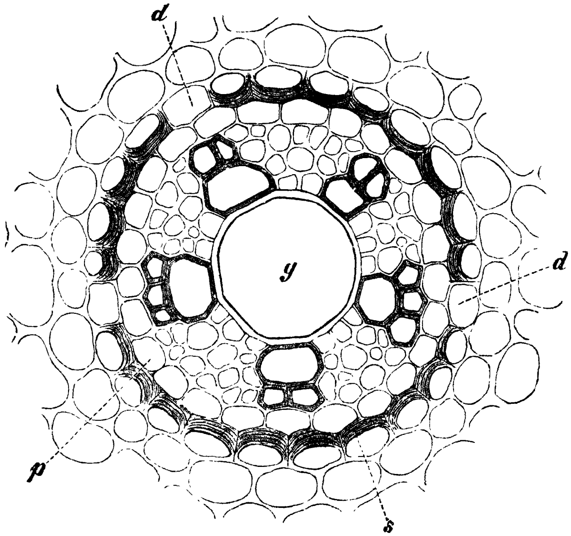

Fig. 156.—Transverse section of the radial bundle of the root of *Allium ascalonicum*. *s*, Endodermis with the inner walls thickened; *d*, transfusion-cells; *p*, pericycle; *g*, large central vessel. (Rothert after Haberlandt.)

Type 1) and, uniting with the portions derived from the adjoining strands of xylem, place themselves internal to the strands of phloem to constitute the collateral bundles (Fig. 157, B). A variant of the second, and more frequent, type is characterised by the phloem-strands as well as the xylem-strands dividing; in this case there are in the stem twice as many collateral bundles as there were xylem- (or phloem-) strands in the root.

4. Branching of the Root.—By this process, in which a root always gives rise to roots, the root-system can penetrate the soil in all directions and obtain from the whole space thus occupied water and dissolved salts.

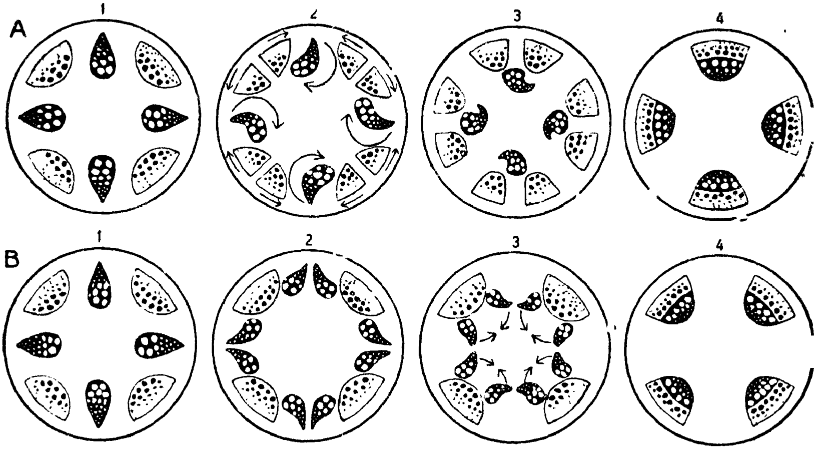

FIG. 157.—The transition from the radial bundle of the root to the collateral bundles of the stem represented diagrammatically, after the descriptions of VAN TIEGHEM and CHAUVEAUD. Cortex and pith, white; phloem, black dots; xylem, white dots on black ground. Further explanation in the text.

DICHOTOMOUS branching by an equal division of the growing point only occurs in some Pteridophyta (Lycopodinae).

With this exception the branching of the root is LATERAL (Fig. 152), the lateral roots, in contrast to the lateral shoots, originating at some distance from the growing point where the meristematic cells have been transformed into permanent tissue. They arise ENDOGENOUSLY (Fig. 158) within the tissues of the parent-root and in acropetal succession. The growing point of the new root is formed from the innermost layer of the cortex in Pteridophytes and from the pericycle in the Phanerogams; a group of parenchymatous cells commences to divide, the cells returning to the meristematic condition. The lateral roots break through the whole thickness of the cortex as they emerge in the order of their development from the main root. The ruptured cortex is frequently recognisable as a sort of collar round the base of the lateral root. Other lateral roots may form subsequently between those already developed and on older parts of the root.

The lateral roots always stand in VERTICAL SERIES on the parent-root (82). This arrangement is determined by their always arising either opposite one of the longitudinally-running strands of xylem (Fig. 158), or opposite the plate of conducting parenchyma which separates a strand of xylem from one of phloem. The number of vertical series of roots is thus either the same as the number of strands of xylem, or twice this.

The structure of the lateral roots corresponds with that of the main root, and the xylem and phloem are continuous from the one to the other.

5. Roots borne on Shoots.—Roots not only arise from other roots but may be developed from the shoot, both from stems and leaves. They are usually endogenous. In Ferns they arise from meristematic tissue in the region of the growing point of the shoot.

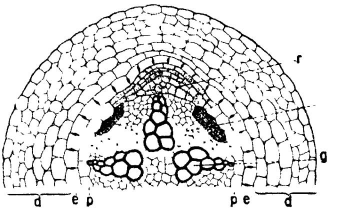

FIG. 158.—Transverse section of the root of *Vicia Faba* showing the origin of a lateral root (*r*). *e*, Endodermis; *p*, pericycle; *d*, cortex; *g*, xylem-strand; *v*, phloem-strand of the radial bundle. (× 40. Somewhat diagrammatic.)

A very usual place for such adventitious roots to arise is at the nodes of the stem; they replace the primary root-system which has been lost when the older part of the plant died off (83). They are especially numerous on the under side of rhizomes (Fig. 139) and creeping shoots. A young shoot, or a cutting planted in moist soil, quickly forms adventitious roots, and roots may also arise in a similar manner from the bases of leaves, especially from *Begonia* leaves when planted in soil (84). Dormant root-rudiments occur in the same manner as dormant buds of shoots. Willow-twigs afford a special case of the presence of such dormant rudiments of adventitious roots, the further development of which is easily induced by darkness and moisture.

6. Appearance of the Root-System. — The lateral roots of successively higher orders are as a rule thinner and grow less strongly than their respective parent-roots. The whole root-system is thus typically RACEMOSE.

The ultimate branches are usually short and have a limited period of existence; they may be termed ABSORBENT ROOTLETS.

The root-system, like the shoot-system, further owes its general appearance to the fact that the main and lateral branches take up distinct positions in space relatively to one another; this depends on differences in their geotropism (cf. p. 341).

Many Dicotyledons (*e.g.* Lupin, Oak) and Gymnosperms (*Abies*) possess a radial MAIN-ROOT or TAP-ROOT (Fig. 152) which, from the seedling onwards, forms the downward continuation of the main stem and grows vertically down into the soil (orthotropous). On this radial lateral roots of the 1st order arise, which penetrate the soil horizontally or obliquely (plagiotropous). The lateral roots of the 2nd order arise in turn on those of the 1st order. They tend to grow on all sides from the latter so that the branches of the root-system penetrate the soil as uniformly as possible in all directions, and, as branching continues, do not leave a cubic centimetre unused. In other Dicotyledons and Gymnosperms (*e.g.* Potato, Pine) the root-system may be more superficial.

A tap-root is usually wanting in Monocotyledons since it becomes arrested in the seedling stage. In its place numerous roots arise from the base of the stem and penetrate the soil vertically, obliquely, or horizontally. They branch monopodially, bearing lateral roots of successively higher orders which penetrate the soil in all directions. In the Wheat, for example, there is no tap-root, but the root-system continues to extend in a horizontal plane.

The length of all the roots of a plant taken together is surprising. Thus for a plant of Wheat it may amount to some hundreds of metres.

Some of the roots of trees in tropical forests are developed in a peculiar fashion. The extraordinarily high and thick stems of many such trees are supported at the base by strong vertically-placed BUTTRESS-ROOTS. In other cases support is given by aerial roots growing down from the branches to the earth and attaining the thickness of woody trunks (PROP-ROOTS, *e.g.* in species of *Ficus*, cf. Fig. 654).

(c) Growth in Thickness of the Cormus

It has been seen that the additions to the root and shoot made by the increase in number of the meristematic cells in the growing points increase in length as they mature. A certain increase in thickness of the parts is associated with this growth in length; this depends on the enlargement of the cells on passing from the meristematic condition and not on increase in their number (PRIMARY GROWTH IN THICKNESS, cf. Figs. 94, 96, 98, 111). This, as a matter of fact, is slight, but is often followed in stems and roots by processes of growth that will now be considered.

The larger the shoot-system becomes the more readily will it escape overshadowing by other plants and form more organic material. Thus in many plants the growth of the small seedling with a few leaves leads, with the accompanying branching, to a cormus of the size of a large tree bearing a very large number of leaves. The increase in the aerial shoot-system and in the number of leaves makes progressively great demands on the water supply from the roots, which can only be met by the increase of surface and the branching of the root-system; in many cases additional roots are developed from the stem. All increase of the root-system, however, depends on a supply of organic food materials manufactured in the leaves. Thus the further development of the crown of foliage and of the root-system are intimately related to one another. The increase in size of the shoot- and root-systems further presupposes that a sufficient number of conducting tracts in the stems and roots can be developed, both for water and for organic materials, and that the stem should be strong enough to support the increasing weight even when exposed to wind. There is thus an intimate connection between the size of the cormus and the formation of conducting tracts in its axes and the rigidity of the shoot.

The rigidity requires to be greater the larger the plant becomes and the longer it lives. Plants or shoot-systems which only live for a limited period and die off after bearing reproductive organs have usually herbaceous structure (HERBS). Large cormi which live for many years and bear fruit repeatedly have as a rule the rigidity of their stems and roots increased by the formation of wood. Such woody plants are called SHRUBS if they do not exceed a moderate height, and retain their lateral shoots so that their branches are formed near the ground. They are called TREES (85), on the other hand, if they attain a greater height, have a main stem or trunk (which must have the type of rigidity possessed by a pillar), and usually lose their lower branches at an early period.

In catalogues and descriptions of plants the duration of the period of growth (86) is usually expressed by special symbols: thus ⊙ indicates an annual; ⚇ a biennial, and ♃ a perennial herb; ♄ is employed to designate shrubs, and for trees the sign ♄ is in use.

The requirements, both as regards the number of conducting tracts and the necessary rigidity, are met in a variety of ways in cormophytic plants.

In the first place, there are plants in which the main axis of the seedling and any lateral branches that arise attain a sufficient thickness and develop sufficient mechanical and conducting tissues before growth in length; when this takes place later the thickness is adequate for the future increase in size of the plant. The primary root in such cases remains thin and usually dies off early, while as many roots as are necessary arise from the basal portion of the shoot. To this FIRST TYPE (87) belong the majority of Pteridophytes and Monocotyledons, including nearly all the forms that have definite stems (Tree-ferns (Fig. 511), Palms, Pandanaceae, certain Liliiflorae).

Thus in such plants as the Palms the embryonic stem remains very short on germination. The primary meristem of the flattened growing point increases in breadth, leading to the axis of the seedling, from which the columnar stem will proceed, having a considerable thickness from an early stage. (Fig. 825.) In such forms as the Palms and Pandanaceae the stem may continue to increase slightly in thickness after the permanent tissues have developed by a process of expansion of the cells. The cells of the sclerenchymatous strands which accompany the phloem of the vascular bundles may thus increase in diameter leading to an enlargement of the strand as a whole. In places this growth in thickness may be accompanied by divisions in parenchymatous cells (*e.g.* in some Palms).

Secondly, there are plants in which long slender stems and roots with only a few conducting and mechanical elements are first developed. A limit would soon be set to the supply of water to the leaves and of nutritive material to the root-system, and thus to the increase in size of the plant, by the small number of conducting elements in the primary stem and root. Provision is, however, made for an increase in the conducting and mechanical tissues corresponding to the needs of the growing plant. This is effected by a continued process of cell division forming secondary tissues and leading to a SECONDARY GROWTH IN THICKNESS of the stem and roots. Secondary tissues are those that are added to or replace the primary tissues as a result of the activity of a secondary meristem or CAMBIUM (cf. p. 44). Such secondary growth occurs in herbaceous as well as in woody plants. The majority of herbaceous and woody Gymnosperms and Dicotyledons and some arborescent Liliiflorae belong to the SECOND TYPE (88). The primary thickening or maturing of the stem and root dependent on the enlargement of cells is in them followed by increase in number of the cells in a special meristematic zone, the cambial ring.

Secondary growth in thickness was present in certain Pteridophytes known to us as fossil remains, but only became of general occurrence in the Gymnosperms and Dicotyledons.

Secondary Growth in Thickness of Monocotyledons.—In some arborescent Liliiflorae (*Dracaena*, *Cordyline*, *Yucca*, *Aloë*) the axis exhibits growth in thickness due to a secondary meristem. This arises in the cortex where it abuts on the central cylinder in which the vascular bundles are scattered in the manner characteristic of Monocotyledons. In transverse sections divisions can be seen to begin in an annular zone of mature cortical cells. In *Dracaena* this happens at a considerable distance from the growing point, but in other cases it may start close to it. A cylindrical meristematic zone, a number of cells deep, is thus formed; the cells are prismatic and fit together without intercellular spaces. As a result of the formation of tangential walls, cells continue to be cut off towards the inside, and later some are formed to the outside. The latter become secondary cortical tissue; the cells to the inside develop into concentric vascular bundles, in which the xylem surrounds the phloem, and parenchymatous tissue with thickened and lignified walls (Fig. 159).

The meristematic cells have a rectangular shape in transverse and radial sections, while in tangential section they are polygonal; they are thus tangentially placed flattened prisms (cf. Fig. 162 *A*, *II*).

True secondary thickening of the root in Monocotyledons is only known in the case of the genus *Dracaena*. The cambial ring arises in the cortex of the root just outside the endodermis.

Secondary Thickening of Gymnosperms and Dicotyledons. 1. Formation, Structure, and Activity of the Cambium in Stems.

—In the open vascular bundles of the Gymnosperms and Dicotyledons the formation of secondary tissues may take place as soon as the primary tissues have matured, or may even begin before this.

The secondary thickening in annual, scrambling, and twining plants often only begins in older internodes which have long attained their full primary size. In the twigs of trees, on the other hand, the secondary growth may start early, even before the primary tissues are fully developed.

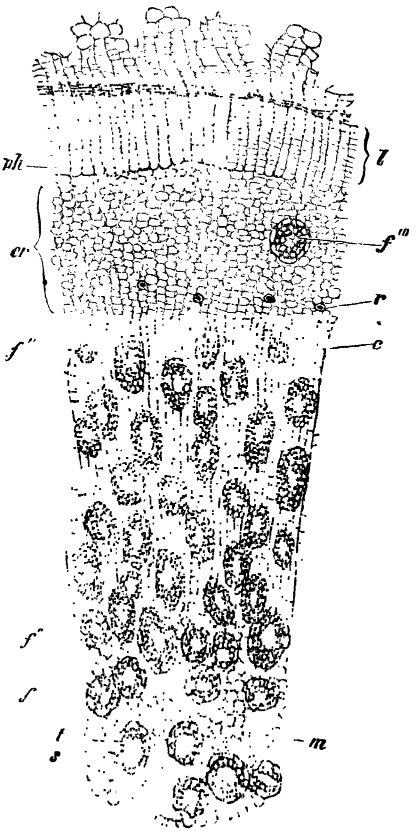

Fig. 159.—Transverse section of the stem of *Cordyline* (*Dracaena*) *rubra*. *f'*, Primary vascular bundles; *f''*, secondary vascular bundles; *f'''*, leaf-trace bundle within the primary cortex; *m*, parenchymatous fundamental tissue; *s*, bundle-sheath; *t*, tracheides; *c*, cambium ring; *cr*, cortex, the outer portion being primary, the inner secondary cortex; *ph*, cork cambium; *l*, cork; *r*, bundles of raphides. (× 30. After Strasburger.)

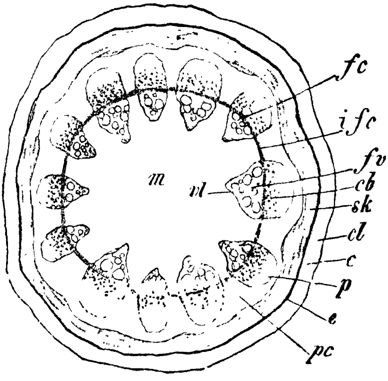

Fig. 160.—Transverse section of a stem of *Aristolochia Sipho* 5 mm. in thickness. *m*, Medulla; *fv*, vascular bundle; *vl*, xylem; *cb*, phloem; *fc*, fascicular cambium; *ifc*, interfascicular cambium; *p*, phloem parenchyma; *pc*, pericycle; *sk*, ring of sclerenchyma; *e*, starch-sheath; *c*, primary cortex; *cl*, collenchyma in primary cortex. (× 9. After Strasburger.)

Only the former case need be considered here, although it is by no means the more frequent (cf. Figs. 160, 161). The primary meristem remaining between the xylem and phloem of the bundle becomes the cambium (Fig. 160, *fc*) and commences again to divide actively.

The vascular bundles are usually arranged in a circle. After the cambial activity has commenced in the bundles, cambium also forms across the medullary rays, by parenchymatous cells dividing tangentially. This INTERFASCICULAR CAMBIUM connects the FASCICULAR

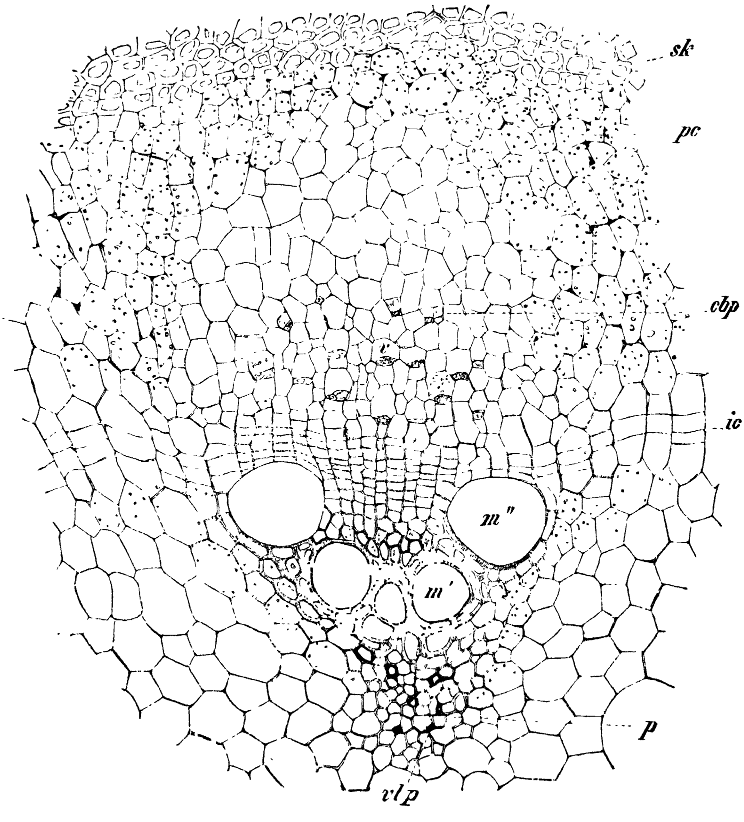

FIG. 161.—Transverse section of a stem of *Aristolochia Sipho* in the first year of its growth, showing a vascular bundle with cambium in active division. *p*, Xylem parenchyma; *vlp*, protoxylem; *m'* and *m''*, vessels with bordered pits; *ic*, interfascicular cambium in continuation with the fascicular cambium; *v*, sieve-tubes; *cbp*, protophloem; *pc*, pericycle; *sk*, inner part of ring of sclerenchymatous fibres. (× 130. After STRASBURGER.)

CAMBIUM within the bundles, forming a complete hollow cylinder of meristematic tissue. The cells grow in the radial direction and undergo division by tangential and by transverse walls.

The cambium-cells fit together without intercellular spaces and form radial rows. They have the shape of elongated prisms more or less flattened tangentially and with both ends pointed; thus the form of the cell appears very different in tangential, radial, or transverse section (Fig. 162). The tangential walls, which form the polygonal or rhombic main faces of the prismatic cell, are thin; the radial walls, on the other hand, are fairly thick and frequently pitted. A middle layer of cells in the cambial zone forms the INITIAL LAYER. Its cells remain permanently in the meristematic condition. They grow in the radial direction, dividing by tangential walls, and so give off daughter-cells (tissue mother-cells) to both sides, but more abundantly on the inner side. These daughter-cells in their turn may undergo tangential divisions, and, often after growing greatly in length and breadth (Fig. 167) and changing their shape, become gradually transformed into permanent cells of the secondary tissues.

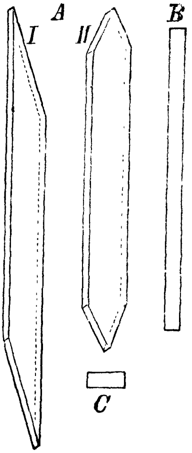

FIG. 162.—Diagrammatic figure of the shape of cambial cells. *A*, *I* and *II*, the two forms which occur, seen in the solid from the tangential face; *B*, in radial section; *C*, in transverse section. (After ROTHERT.)

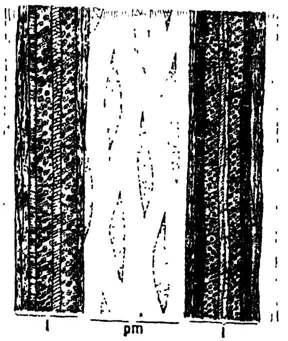

FIG. 163.—A diagrammatic tangential section to illustrate the subdivision of a primary medullary ray into many smaller rays on the commencement of secondary thickening. *l*, *l*, Adjoining primary vascular bundles; *pm*, primary medullary ray transformed by the activity of the interfascicular cambium into many small spindle-shaped medullary rays and reticulately-connected secondary vascular bundles.

The cambium in giving off cells inwards must itself, as the stem grows in thickness, be carried gradually outwards. The circumference of the cambial ring must therefore be increased. This can only be effected by growth and increase in number of the cells in a tangential direction. This comes about by radial division of some of the cells. In other cases the number of cells in the tangential direction is increased by an initial cell of the cambium dividing transversely, and the ends of the two resulting cells becoming placed side by side tangentially by sliding growth (89).

All the permanent tissue formed on the inner side of the cambium is termed WOOD; this is usually hard and composed of more or less lignified cells. The tissue formed to the outside by the cambium usually consists mainly of unlignified cells and is termed the BAST.

The secondary tissue formed internally by the fascicular cambium resembles the xylem, and that to the outside the phloem of the primary vascular bundle. By the activity of the interfascicular cambium the primary medullary rays are continued through the wood and the bast. Their breadth is, however, usually diminished, since the interfascicular cambium in great part gives rise to tissues similar to those formed by the fascicular cambium. Thus, in place of the original broad medullary rays, the cambium forms at definite points narrower radial rows of medullary ray tissue. These medullary rays, which are spindle-shaped when cut across (Fig. 163), traverse the wood and the bast, connecting the pith with the cortex as PRIMARY MEDULLARY RAYS. As the thickness of the secondary wood and bast increases, SECONDARY MEDULLARY RAYS are developed from the fascicular cambium. In one direction the secondary medullary rays end blindly in the wood and in the other in the bast; the later they develop the less deeply do they penetrate the tissues on either side of the cambium (Fig. 172).

The cambial cells which give rise to medullary rays are shorter and their end walls are more horizontal, for when a medullary ray is to be initiated the ordinary cambium-cell becomes divided transversely or obliquely.

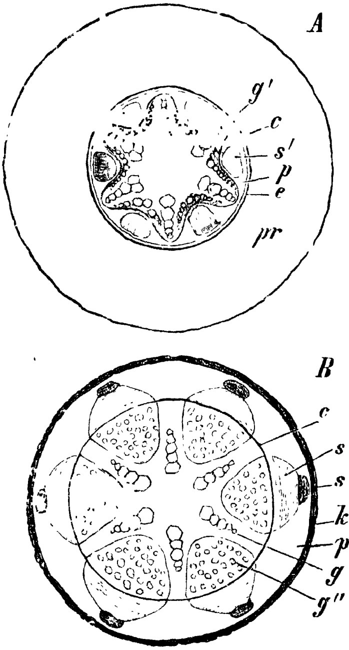

FIG. 164.- Diagrammatic representation of the growth in thickness of a dicotyledonous root. *pr*, Primary cortex; *c*, cambium ring; *g'*, primary vascular strand; *s'*, primary phloem-strand; *p*, pericycle; *e*, endodermis; *g''*, secondary wood; *s''*, secondary bast; *k*, periderm. (After STRASBURGER.)

The origin of the cambium and the nature of its activity can be distinguished into three main types (99) according to the primary construction of the stem: 1. The stem has a circle of collateral vascular bundles separated from one another by broad medullary rays; the breadth of the medullary rays is maintained during secondary growth, the interfascicular cambium producing only medullary ray tissue. This is the case for many herbaceous plants, but among woody plants is only found in lianes (*e.g.* *Aristolochia*). In those herbs in which the inner portion of the medullary rays between the primary strands of xylem consists of sclerenchyma (cf. p. 91), the interfascicular cambium forms similar tissue on its inner side. 2. The stem as in the first type has a circle of collateral leaf-trace bundles separated by broad medullary rays. Before the primary growth in thickness is completed there arise from the still meristematic tissue of each medullary ray, that now assumes the characters of a cambium, one or a number of small, cauline, intermediate bundles which anastomose tangentially; the intervening meshes are occupied by narrow primary medullary rays that are spindle-shaped when cut across (Fig. 163). The original medullary rays become filled up in this way in many herbaceous and woody plants. 3. In the transformation of the primary meristem to permanent tissue there arises, instead of a circle of collateral bundles, a vascular tube, which appears like a concentric bundle with a central pith and internally-situated xylem. There is a layer of meristematic tissue between the xylem and phloem that later becomes the cambium. The vascular tube may be traversed by very narrow spindle-shaped primary medullary rays, or these may be completely wanting. This type is found in many trees.

The primary xylem of the bundles in stems which have undergone secondary thickening projects into the pith.

2. Formation and Activity of the Cambium in the Root.—As has been seen (Fig. 154), the strands of xylem and phloem alternate in the central cylinder of the root; they are separated by intervening parenchymatous tissue. When secondary thickening begins in such a root cambial layers arise internal to the strands of phloem, and between these and the strands of xylem, by divisions taking place in some of the parenchymatous cells; the cambium forms wood towards the centre and bast towards the outside. These arcs of cambium meet in the pericycle just outside the xylem-strands and the cambial ring is completed from the pericycle. The wavy outline of this is shown in Fig. 164 *A*; by the activity of the cambium in producing new tissues the depressions in the ring are soon evened out (Fig. 164 *B*). The secondary wood and bast of the root have the same structure as the corresponding tissues in the stem. A cross-section of a root in which the secondary growth has continued for some years can scarcely be distinguished from a cross-section of a stem; by careful examination, however, the characteristic strands of primary xylem can be recognised in the centre of the root.

Repeated Formation of Cambium in Stems and Roots.—Deviations from the usual type of secondary growth as found in most Gymnosperms and Dicotyledons are met with in some cases. These anomalous types (102) are characterised by differences in the distribution and in the activity of the cambium.

In some Cycadeae and certain species of *Gnetum* among the Gymnosperms and in the Chenopodiaceae, Amarantaceae, Nyctaginaceae, Phytolaccaceae, and some other families of Dicotyledons, the first ring of cambium, which arose in the usual way, ceases to function after a time. A new zone of cambium forms, usually in the pericycle, *i.e.* external to the bast, or else in tissue derived from the earlier cambium. The new cambium forms bast externally and wood internally, these tissues being traversed by medullary rays. Its activity in turn comes to an end and its place is taken by a new cambium formed outside this zone of bast. The process can be repeated and leads to the production of concentric zones each composed of wood and bast. This is seen, for example, in the transverse section of the stem of *Mucuna altissima*, a liane belonging to the Papilionaceae which is represented in Fig. 165. Such concentric zones of wood and bast are met with in some succulent roots which persist for two or more vegetative periods. This is the case in the Beet (*Beta vulgaris*), where the zones can be readily recognised with the naked eye on cross-sections. They arise as described above, but, as in the case of the typical secondary growth of other succulent roots, parenchymatous tissue which serves for storage of reserve materials forms a large proportion of the newly-developed tissues.

3. The Wood. A. Kinds of Tissue and their Functions.—The construction of the wood is complex, and in Dicotyledons it is usually composed of three distinct types of tissue the walls of which are more or less lignified. These are: (1) longitudinally-running strands of dead VESSELS (Fig. 166 *g*, *tg*); (2) longitudinally-running strands of sclerenchymatous fibres, WOOD-FIBRES (*h*), that are usually dead; (3) STORAGE AND CONDUCTING PARENCHYMA (*hp*), which forms longitudinally-running strands, and in the medullary rays is also directed radially; this constitutes the WOOD-PARENCHYMA and PARENCHYMA OF THE MEDULLARY RAYS. Corresponding to this the wood serves (1) for water-conduction, (2) to render the stems and roots rigid against pressure and bending, and (3) for the storage of organic materials. The properties which make wood such a valuable building material depend upon its natural function as a mechanical tissue.

The various kinds of cells of which the wood is composed can be most readily studied by treating wood with SCHULTZE's macerating mixture (cf. p. 40).

The vessels are pitted or less-commonly reticulately thickened. The tracheae may be wide and composed of short segments, or narrow and formed of more or less elongated cells (Fig. 166 *g*, *tg*); the tracheides are narrow and elongated and serve both for conduction and as mechanical tissue. The wood-fibres (*h*) are usually very long and narrow, pointed at both ends, and with thick walls provided with narrow oblique pits. The cells of the parenchyma (*hp*) are rectangular and prismatic or are spindle-shaped; they are usually elongated in the direction of the long axis and have either thin or thick walls with small, circular, simple pits. They contain abundant reserve materials (starch, oil, or sugar). Intercellular spaces only occur in the parenchymatous strands.

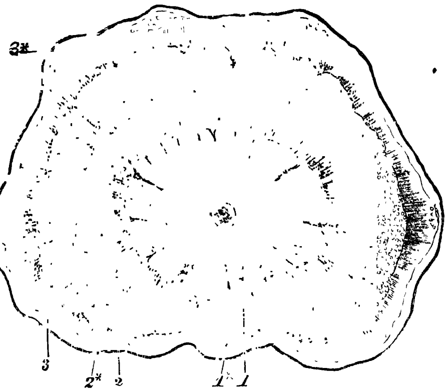

FIG. 165.—Transverse section of the stem of *Mucuna altissima*. *1*, *2*, *3*, Successively-formed zones of wood; *1**, *2**, *3**, successively-formed zones of bast. (¾ nat. size. After SCHENCK.)

The tracheides and wood-fibres are frequently more than 1 mm. in length and are considerably longer than the cambial cells from which they arose. This increased length, like the increased width of the larger tracheae, is attained by sliding growth (p. 44; Fig. 167). In the formation of wood-parenchyma the cambial cells undergo repeated transverse divisions. The resulting parenchyma thus consists of rows of cells, the origin of which from a cambial cell is indicated by the row ending above and below in a pointed cell (Fig. 166 *gh*, *hp*).

The walls between cells of the wood-parenchyma or medullary rays and the vessels have bordered pits on the side towards the vessel only; the pits in the living cells have no border. The walls separating vessels and wood-fibres and those between the latter and parenchyma-cells are, on the other hand, usually without pits.

In woods composed of vessels, wood-fibres, and parenchyma there are frequently transition forms between the typically-constructed elements, and there is a corresponding lack of sharp distinction as regards function. Narrow tracheae (Fig. 166 *tg*) lead on to the tracheides (Fig. 166 *gt*, *t*). Narrow, sharply-pointed tracheides (fibre-tracheides, *ft*), the function of which is mainly mechanical, form the transition to the wood-fibres (*h*). Slightly thickened wood-fibres which retain their living contents (*ef*) and are either without or with transverse walls (*gh*) form the transition to the cells of the wood-parenchyma (*hp*). According to STRASBURGER ([61]) the fibre-tracheides are to be derived phylogenetically from the vessels and the wood-fibres from wood-parenchyma.

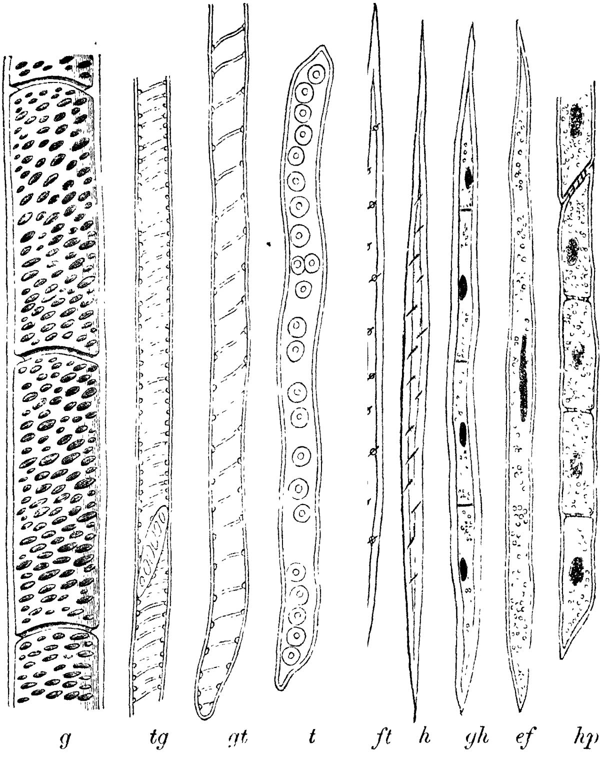

FIG. 166.—Tracheae, tracheides, wood-fibres, and wood-parenchyma of a Dicotyledon with transition-forms between the various elements. Diagrammatic. Explanation in text. (Modified after STRASBURGER.)

In the wood of **Gymnosperms** there are only tracheides with typical bordered pits, together with some wood-parenchyma and a considerable amount of parenchyma of the medullary rays. The division of labour is here less advanced, the same elements being concerned with the mechanical and water-conducting functions. *Drimys*, belonging to the Magnoliaceae, is a Dicotyledon with wood composed of tracheides and parenchyma only.

B. Arrangement of the Tissues in the Wood.—In the Gymnosperms (Figs. 168-170) the wood of the stems and roots has thus a relatively simple structure. The tracheides are arranged in regular radial rows (Fig. 168 *A*), in correspondence with their mode of origin (Fig. 168 *B*). Since they increase in size mainly in the radial direction, and hardly at all in the tangential and longitudinal directions, they retain the same form as the cambial cells (Fig. 162). They have large, circular, bordered pits frequently only upon their radial walls; the pits are thus seen in surface view in radial sections (Figs. 67 *B*, 68 *A*).

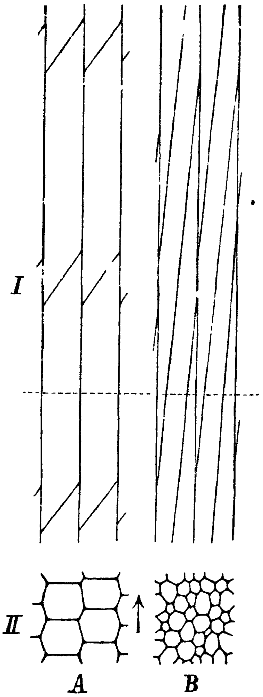

FIG. 167.—Diagrammatic representation of sliding growth, of wood-fibres. *I*, In tangential longitudinal section; *II*, in transverse section along the dotted line in *I*. *A*, *I*, *II*, cells in the young condition; *B*, *I*, *II*, after sliding growth has taken place. (After ROTHERT.)

In the wood of the Pines, Firs, and Larches parenchyma is found only around schizogenous resin-canals which run longitudinally in the wood (Figs. 168 *A*, *h*; 172 *h*), and are connected by others which run radially in some of the broader medullary rays. For this reason considerable amounts of resin flow out from the wounded stem of a Pine or Fir. In the other Conifers the wood-parenchyma is limited to simple rows of cells, the cavities of which may later become filled with resin.

The medullary rays in the wood of Gymnosperms are numerous, and for the most part only one layer of cells broad (Figs. 168 *m*, 170 *sm*, *tm*; 172 *ms*). The cells of the medullary ray are elongated in the radial direction; they contain abundant starch and are associated with intercellular spaces (Fig. 170 *i*). They serve to transfer the products of assimilation, formed in the leaves and conducted downwards in the bast, in a radial direction into the wood of the stem or root, where storage takes place; they also conduct water from the wood outwards. The medullary rays are suited to perform these functions, since, as has been seen, they extend into both the wood and the bast (Figs. 168 *B*, 169, 172). The intercellular spaces communicate with the intercellular system of the cortex and allow of the necessary gaseous exchanges between the living cells in the wood and the external atmosphere.

In certain Gymnosperms, especially the Pines, single rows of cells of the medullary ray in the wood (usually the marginal rows) are tracheidal and without living contents; they are connected with one another and with the tracheides by means of bordered pits (Fig. 169 *tm*). They are protected against compression by the living turgescent cells of the medullary ray by means of special thickening of their walls. These tracheidal cells facilitate the conduction of water in the radial direction between the tracheides, which are only pitted on their radial walls. In most other Conifers, in which such tracheidal elements in the medullary rays are wanting, there are tangentially-placed bordered pits in the tracheides of the wood, and these allow of the movement of water in a radial direction. The parenchymatous cells of the medullary rays of the wood are connected with the tracheides by means of large pits bordered on one side (Fig. 170 *ct*).

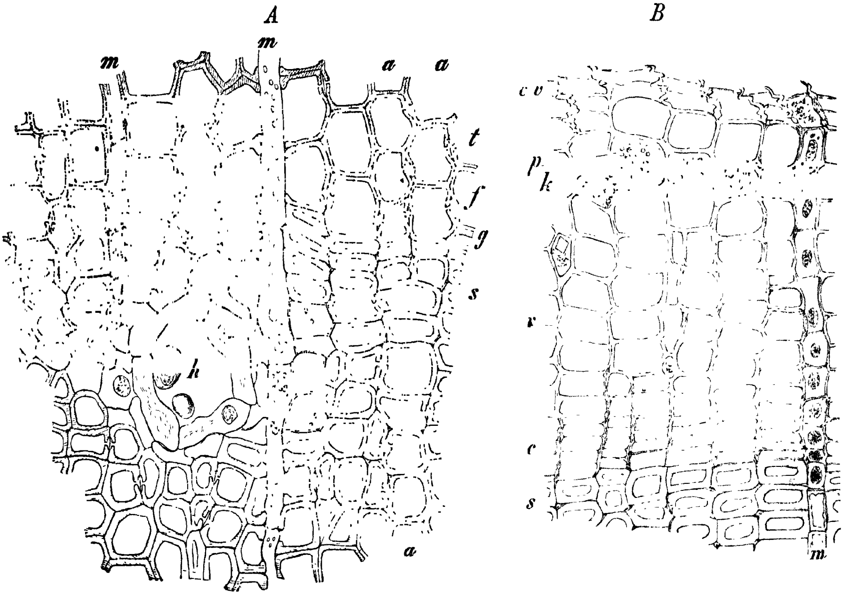

FIG. 168.—*A*, Transverse section of the wood of a Pine at the junction of two annual rings. *f*, Spring-wood; *s*, autumn-wood; *t*, bordered pit; *e*, interposition of a new row of tracheides; *h*, resin canals; *m*, medullary rays; *g*, limit of autumn-wood. (× 240.) *B*, Part of a transverse section of the stem of a Pine. *s*, Late wood; *c*, cambium; *v*, sieve-tubes; *p*, bast-parenchyma; *k*, cell of bast-parenchyma containing crystal; *cv*, sieve-tubes, compressed and functionless; *m*, medullary ray. (× 240. After SCHENCK.)

Owing to climatic variations, the cambial tissue of Gymnosperms, as of most Dicotyledons, exhibits a periodical activity which is expressed by the formation of ANNUAL RINGS (94) of growth (Figs. 171, 172). In spring, when new shoots are being formed, wider and thinner-walled tracheal elements are developed than later in the season. For this reason a difference is perceptible between the EARLY WOOD (spring-wood), which is composed of large elements especially active in the conveyance of water (Figs. 168 *A*, *f*, 172 *f*), and the LATE WOOD (autumn-wood), consisting of narrow elements which impart to a stem its necessary rigidity (Figs. 168 *A*, *s*, 172 *s*). Throughout the greater part of the temperate zone, the formation of wood ceases in the latter part of August until the following spring, when the larger elements of the spring-wood are again developed. Owing to the contrast in the structure of the spring- and the autumn-wood, the limits (Figs. 168 *g*, 172 *i*) between successive annual rings of growth become so sharply defined as to be visible even to the naked eye, and thus serve as a means of computing the age of a plant.

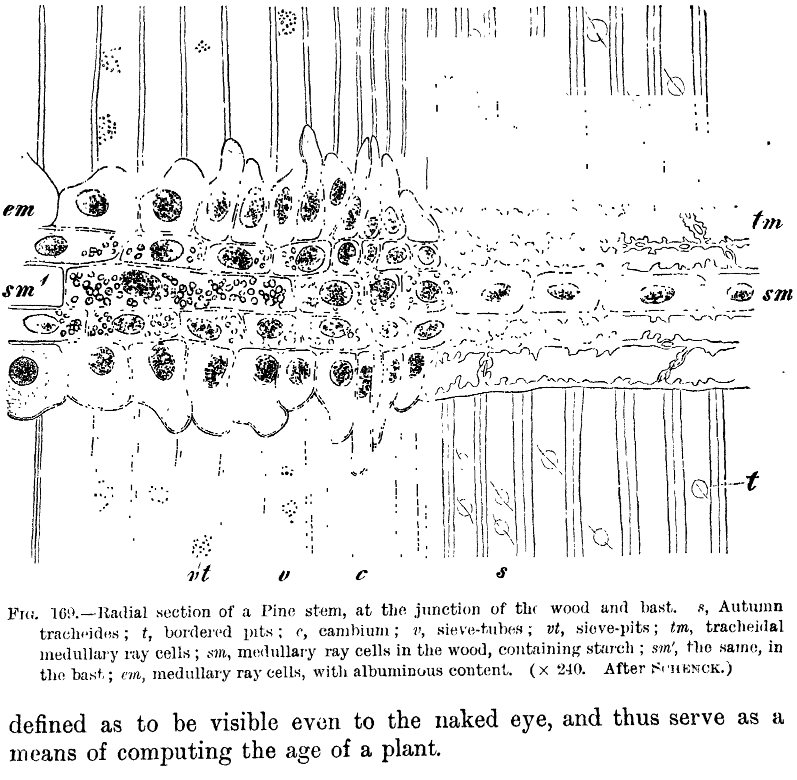

FIG. 169.—Radial section of a Pine stem, at the junction of the wood and bast. *s*, Autumn tracheides; *t*, bordered pits; *c*, cambium; *v*, sieve-tubes; *vt*, sieve-pits; *tm*, tracheidal medullary ray cells; *sm*, medullary ray cells in the wood, containing starch; *sm'*, the same, in the bast; *em*, medullary ray cells, with albuminous content. (× 240. After SCHENCK.)

In a stem or root that has undergone secondary thickening fewer annual rings will be seen on the cross-section the nearer this is made to the growing point. The older annual rings and the older layers of bast disappear in order of their age as the tip is approached.

Under certain conditions the number of annual rings may exceed the number of years of growth. When the leaves are destroyed by frost, caterpillars, or other injurious influences, the buds destined for the succeeding spring may unfold, and the formation of the new foliage brings about a second formation of spring wood. On the other hand, woody plants that usually have definite annual rings may exceptionally show a smaller number of rings than that corresponding to their age, owing to the limits between some of the rings not being clearly marked. In this way the number of rings on one radius of the stem may be less than when they are counted on another radius.

The annual rings are usually not clear in the secondary wood of roots.

The wood of the stems and roots of **Dicotyledons** can be readily distinguished from that of a Gymnosperm even when only slightly magnified (Figs. 173-175). Not only are wood-fibres and usually wide tracheae present, in addition to tracheides and parenchyma, but the unequal growth of the various component elements leads to a departure from their original radial arrangement. In the spring-wood there are numbers of very wide tracheae (Figs. 173, 174 *m*), while narrow wood-fibres (*l*) and fibre-tracheides (*t*) predominate in the autumn-wood.

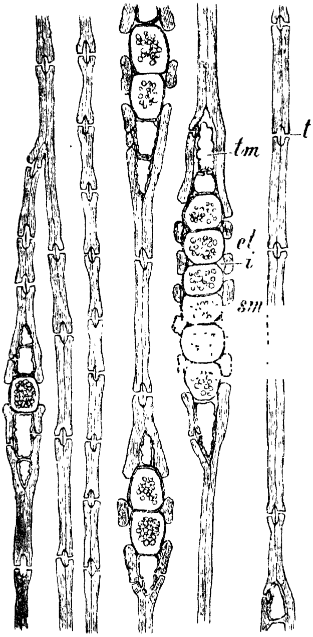

FIG. 170.—Tangential section of the autumn wood of a Pine. *t*, Bordered pit; *tm*, tracheidal medullary ray cells; *sm*, medullary ray cells containing starch; *et*, pit bordered only on one side; *i*, intercellular space in the medullary ray. (× 240. After SCHENCK.)

In the woody plants of tropical regions, when there is no seasonal interruption of growth, annual rings may be wanting, but in many cases zones resembling the annual rings occur indicating a periodic activity of the cambium.

The water-conducting elements of the most recently formed annual rings are the only ones that are in direct connection with the leaves of the corresponding period of vegetation. Since there is a sudden demand for a considerable amount of water for transpiration when the leaves unfold in the spring, the provision of conducting channels in the spring-wood is readily comprehensible. In many woody plants the foliage is not further increased during the summer, and the cambium can therefore form mechanical tissue in the autumn-wood.

In spite of the variety in the structure of the wood of Dicotyledons there are some constant features in the arrangement of the different tissues. The vascular strands composed of tracheae and tracheides, while they ramify in the radial and tangential directions, form continuous longitudinal tracts from the roots to the finest tips of the branches. Were this not so the needs of the shoot-system as regards its water-supply would not be met.

WOOD-PARENCHYMA (Figs. 173, 174 *p*), which is well developed in most dicotyledonous woods, also forms longitudinal strands or layers which, however, end blindly above and below. These form, along with the medullary rays, a connected system of living cells. The vessels always stand in connection with these living cells, being sometimes surrounded by them and in other cases in contact with them on one side (Fig. 173 *p*).

The MEDULLARY RAYS (Figs. 171 *pm*, *sm*; 173, 174 *r*) resemble those of the Gymnosperms in being radially-placed bands of tissue, of greater or less vertical height, and one or a number of cells in breadth; they may be branched or unbranched (Fig. 175 *tm*). They are continuous across the cambium into the bast (Fig. 178). The vascular strands are in contact with them at places. The parenchyma of the medullary rays thus connects the parenchyma of the bast with that of the wood, and unites all the living tissue of the stem and root into a single system provided with intercellular spaces. Assimilated material moving downwards in the bast can thus pass radially into the wood and be carried in this for some distance upwards or downwards, to be stored as starch or fat in the living parenchymatous cells. In spring when the buds are unfolding much of this reserve material is passed into the vessels in the form of glucose and small amounts of albuminous substances. In this way these substances can be transported rapidly to the places where they are to be utilised. Thus, during the winter and in early spring, sugar and albumen can be demonstrated in the

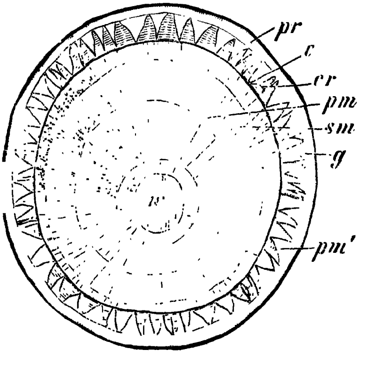

FIG. 171.—Transverse section of a stem of *Tilia ulmifolia*, in the fourth year of its growth. *pr*, Primary cortex; *c*, cambium ring; *cr*, bast; *pm*, primary medullary ray; *pm'*, expanded extremity of a primary medullary ray; *sm*, secondary medullary ray; *g*, limit of third year's wood; *m*, pith (×6. After SCHENCK.)

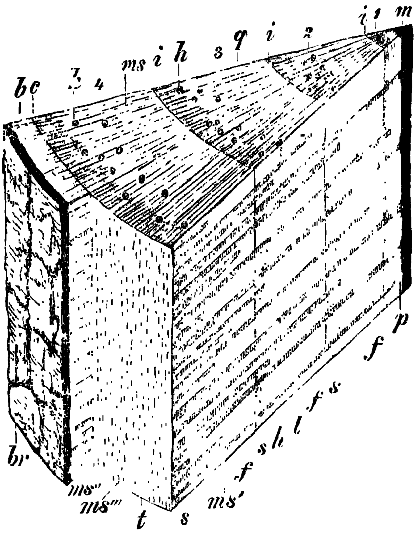

FIG. 172.—Portion of a four-year-old stem of the Pine, *Pinus sylvestris*, cut in winter. *q*, Transverse view; *l*, radial view; *t*, tangential view; *f*, spring wood; *s*, autumn wood; *m*, medulla; *p*, protoxylem; *1*, *2*, *3*, *4*, the four successive annual rings of the wood; *i*, junction of the wood of successive years; *ms'*, *ms'''*, *ms*, medullary rays in transverse, radial, and tangential view, *ms''*, radial view of medullary rays in the bast; *c*, cambium ring; *b*, bast; *h*, resin canals; *br*, bark, external to the first periderm layer, and formed from the primary cortex. (× 6. After SCHENCK.)

vessels or in the sap which readily exudes from cut stems of Birch, Sycamore, and other trees.

The intervals between the strands of vessels and of parenchyma and the medullary rays are occupied by strands of wood-fibres (sclerenchyma).

The height and breadth of the medullary rays are most readily seen when they are cut across in tangential longitudinal sections of the stem ; the rays then appear spindle-shaped (Fig. 174 *r*). In most woods their size varies only within narrow limits, but in others, such as the Oak and the Beech, the range is greater. In some lianes (*e.g. Aristolochia*) the primary rays are particularly wide and high, and may extend for the length of a whole internode.

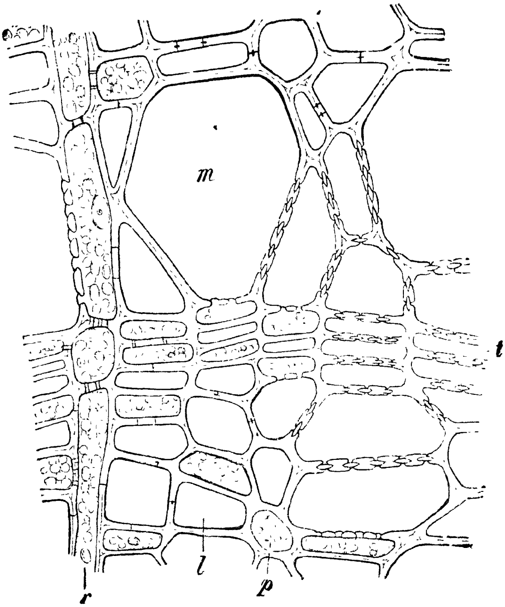

FIG. 173.—Portion of a transverse section of the wood of *Tilia ulmifolia*. *m*, Large pitted vessel; *t*, tracheides; *l*, wood-fibre; *p*, wood-parenchyma; *r*, medullary ray. (× 540. After STRASBURGER.)

Grain of the Wood.—The technical value of certain woods is affected not only by the colour but by the graining. This depends in the first place on the arrangement of the annual rings and medullary rays, but also in many cases (*e.g.* Hazel) upon a wavy course of the elements of the wood ; this may be brought about by the crowded arrangement of lateral or adventitious buds or lateral roots, or by the stimulus of wounding.

C. Subsequent Alterations of the Wood.—In the majority of trees the living elements in the more centrally-placed older portions of the woody mass die and the water-channels become stopped up, leading to the formation of what is known as the HEART-WOOD. Only the outer layer of the wood composed of the more recently-formed annual rings thus contains living cells and constitutes the SPLINT-WOOD. Reserve materials can only be stored in the splint-wood, and water-conduction is also limited to this and indeed to its outermost portion, since, as has been seen, it is only the peripheral vessels that are in connection with the leaves and the youngest lateral roots. The heart-wood serves only for strength. The heart-wood is usually darker in colour than the splint-wood and is also denser, harder, and stronger; it is protected against decay by impregnation with various substances. In other cases the heart-wood is not distinct in colour from the splint-wood and readily decays; this leads to the hollow stems so often found in old Willows.

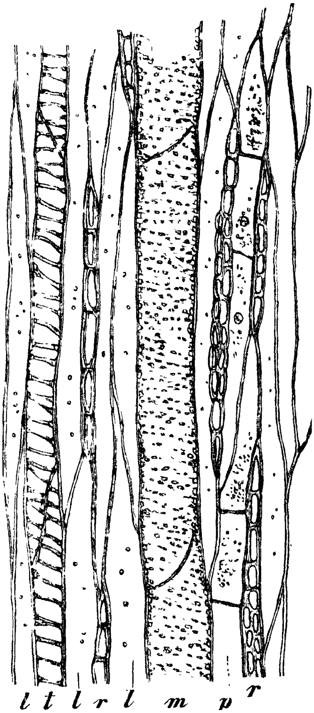

FIG. 174.—Tangential section of the wood of *Tilia ulmifolia*. *m*, Pitted vessel; *t*, spiral tracheides; *p*, wood-parenchyma; *l*, wood-fibres; *r*, medullary rays. (× 160. After SCHENCK.)

The whitish-yellow splint-wood contrasts most strongly with the heart-wood when the latter is dark in colour; thus in the Oak it is brown and in the Ebony (*Diospyros*) black. The heart-wood appears to be more durable the darker it is. Before their death the living cells of the wood, which lose their reserve materials, usually form various organic substances, especially tannins, which impregnate the walls of the surrounding elements, while resinous and gum-like products accumulate in the cavities. The tannins preserve the dead wood from decay, and their oxidation products give its dark colour. The vessels are sometimes occluded by accumulations of gum, and at other times by cells which fill up the lumen more or less completely, and are spoken of as THYLOSES (92) (Fig. 176); they originate by the adjoining living cells growing into the vessels through the pits, the membrane of which they press inwards. Thyloses also form in wounded vessels and occlude the lumen. Inorganic substances are not uncommonly deposited in the heart-wood; thus calcium carbonate occurs in the vessels of *Ulmus campestris* and *Fagus sylvatica*, while amorphous silicic acid is deposited in the vessels o Teak (*Tectona grandis*). Colouring matters are obtained from the heart-wood of some trees, *e.g.* Haematoxylin from *Haematoxylon campechianum L.* (Campeachy-wood, Logwood).

4. The Bast. A. Kinds of Tissue and their Functions.—Three types of tissue can also be distinguished in the bast (Figs. 168

B, 177): (1) Longitudinally-running strands of SIEVE-TUBES with, in the Dicotyledons, COMPANION-CELLS (Fig. 177 *c*); (2) in many plants longitudinal strands of SCLERENCHYMATOUS FIBRES (BAST-FIBRES) that are as a rule dead (Fig. 177 *l*); and (3) PARENCHYMA with intercellular spaces arranged both longitudinally (*p*) and in the medullary rays (Figs. 168 *B*, *m*; 177 *r*). In addition SECRETORY CELLS of various kinds may be present containing crystals (*k*) or latex. The bast, like the phloem of the vascular bundles, serves mainly to conduct the products of assimilation. It also is of use for the storage of organic substances and frequently as a mechanical tissue. In many plants the sieve-tubes have oblique end-walls (Fig. 177 *v**); they are thin-walled and unlignified, contain proteids, and usually remain functional only for a short period. The bast-fibres are long and narrow and have strongly-thickened walls that may be lignified or not. The parenchymatous cells are elongated in the direction of the strand; they are living cells with abundant reserve materials and thin unlignified walls.

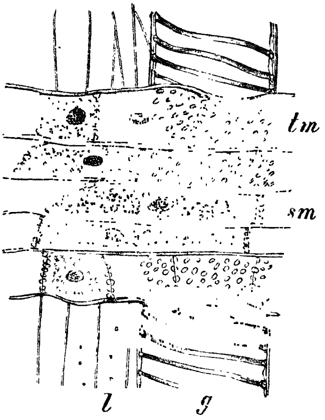

FIG. 175.—A radial section of the wood of *Tilia ulmifolia*, showing a small medullary ray. *g*, Vessel; *l*, wood fibres; *tm*, medullary ray cells in communication with the water-channels by means of pits; *sm*, conducting cells of the medullary ray. (× 240. After SCHENCK.)

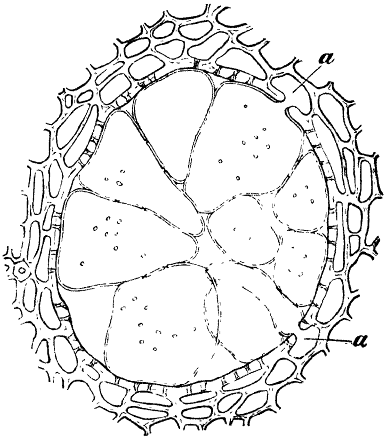

FIG. 176.—Transverse section of a vessel from the heart-wood of *Robinia Pseudacacia*, closed by thyloses; at *a*, *a* is shown the connection between the thyloses and the cells from which they have been formed. (× 300. After SCHENCK.)

At a certain distance from the cambium the sieve-plates become overlaid by callus. Still further out the sieve-tubes and their companion-cells become empty and compressed (Fig. 168 *B*, *cv*).

B. Arrangement of the Tissues in the Bast.—This resembles the arrangement in the wood. The strands of sieve-tubes form branched tracts in which the sieve-tubes have a continuous course from the roots to the foliage. The sieve-tubes, and the longitudinally-running bast-parenchyma, are related at intervals to the medullary rays (Fig. 172 *ms″*), which have been seen to be the continuation of the medullary rays of the wood. Thus the products of assimilation from the foliage can either pass in the bast towards the roots or through the medullary rays to be stored in the living cells of the wood.

The different tissues of the bast are often arranged in very regular tangential bands only interrupted by the medullary rays (Fig. 177). The periodicity of the cambium is not, however, evident in the bast, and

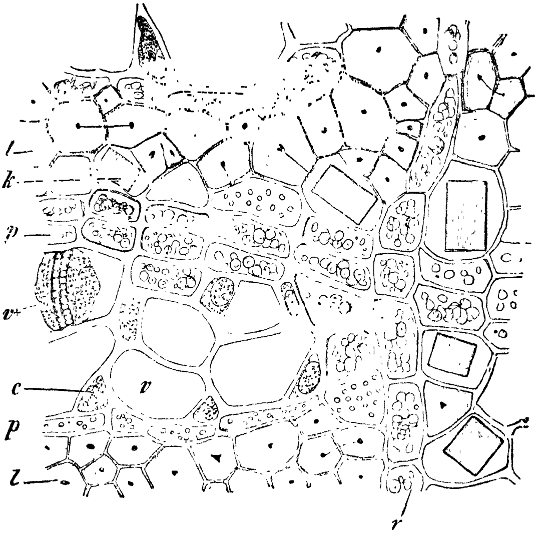

FIG. 177.—Portion of a transverse section of the bast of *Tilia ulmifolia*. *v*, Sieve-tubes; *v**, sieve-plate; *c*, companion-cells; *k*, cells of bast-parenchyma containing crystals; *p*, bast-parenchyma; *l*, bast-fibres; *r*, medullary ray. (× 540. After STRASBURGER.)

there are no annual rings. The cambium continues to produce bast after the formation of the autumn-wood has ceased, for so long as the climatic conditions permit.

In the Lime, for example (Fig. 177), there is an alternation of zones of sieve-tubes (*v*) with companion-cells (*c*), starch-containing bast-parenchyma (*p*), cells containing crystals (*k*), bast-fibres (*l*), and flattened cells of bast-parenchyma (*p*), followed again by sieve-tubes. The differences in the appearance of the bast of different woody plants are due to the greater or less diameter of the sieve-tubes, the presence or absence of bast-fibres, and to the mode of arrangement of the various elements.

In the Pine and various other Abietineae, rows of cells with abundant albuminous contents occur at the edges of the medullary rays (Fig. 169 *em*). They are in close contact with the sieve-tubes and connected with them by sieve-pits, and become empty and compressed at the same time as the sieve-tubes.

Effect of the Secondary Thickening on the Tissues external to the Cambial Ring. 1. Dilatation.—Since the cambium continues to form wood to the inside, and bast to the outside, the stem or root exhibits a secondary increase in thickness. Those permanent tissues which are situated externally to the cambial ring (the epidermis, cortex, primary phloem, and the bast) are naturally affected by this. They are tangentially stretched, compressed, displaced, or torn; they may also grow in the tangential direction (DILATATION). This latter process is naturally limited to the living cells of the cortex, the phloem, and the bast, including those of the medullary rays; in some woody plants even the epidermal cells take part in the dilatation (93). All these cells may grow considerably in the tangential direction and then become divided by radial walls. In the bast such growth is frequently very marked in the case of the medullary rays; in the Lime this leads to the formation of a secondary meristem which gives off rows of parenchymatous cells to either side in the tangential direction, so that the medullary rays of the bast widen year by year towards the outside (Fig. 171 *pm'*). The sieve-tubes and their companion-cells, which only remain functional for a short time and then die, are compressed along with the secretory cells. The sclerenchymatous cells of the cortex and bast, which are usually non-living elements, also take no part in the dilatation. When a hollow cylinder of sclerenchyma is present in the

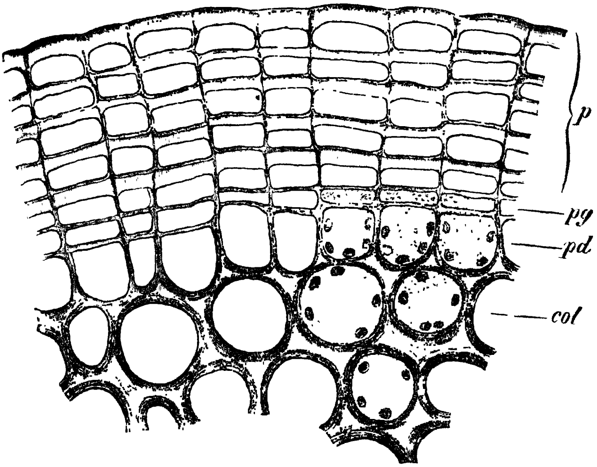

FIG. 178.—Transverse section of the outer part of a one-year-old twig of *Pyrus communis* made in autumn. It shows the commencement of the formation of the periderm. *p*, Cork; *pg*, phellogen; *pd*, phelloderm; *col*, collenchyma. The cork cells have their outer walls thickened and have brown dead contents. (× 500. After SCHENCK.)

cortex (Fig. 179 *sc*), it becomes torn in the tangential direction; the parenchymatous cells grow into the spaces, and in many plants become transformed into thick-walled stone-cells (Fig. 179 *s*). Parenchyma-cells, or groups of them in the cortex and bast, may also be developed as sclerenchymatous cells during the process of dilatation.

The epidermis may continue to expand for years in some species of Rose, Acacia, Holly, and Maple, and in the Mistletoe. The outer walls of the cells are usually strongly thickened, and when ruptured on the surface become reinforced by new layers of thickening deposited within.

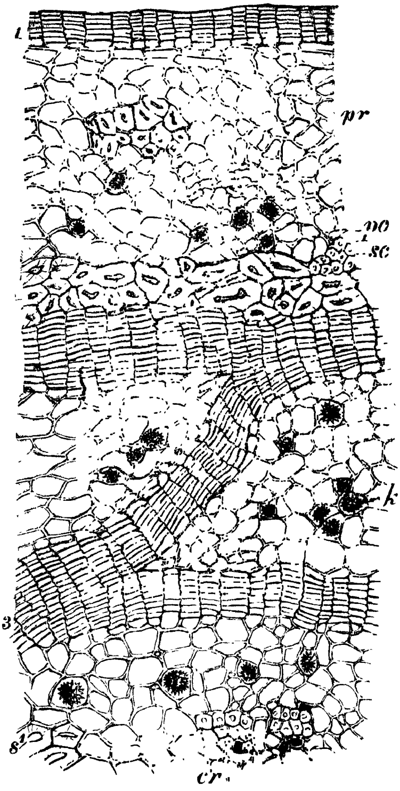

FIG. 179.—Transverse section of the peripheral tissues of the stem of *Quercus sessiliflora*. *1, 2, 3*, Successively formed layers of cork; *pr*, primary cortex, modified by dilatation; *pc*, pericycle; *sc*, sclerenchymatous fibres from the ruptured ring of sclerenchymatous fibres of the pericycle *s*, subsequently formed sclereides; s^1, sclereides, in secondary growth; *cr*, bast fibres; *k*, cells with aggregate crystals. All the tissue external to the innermost layer of cork is dead and discoloured and has become transformed into bark. (× 225. After SCHENCK.)

2. Periderm.—As a rule, however, the epidermis does not take part in the dilatation but is passively stretched and ultimately ruptured. A new limiting tissue is formed some time before this to protect the underlying tissues from drying up. This arises as the CORK (cf. p. 55) by the activity of a special, secondary meristem, situated at the periphery of the organ (Fig. 178).

This CORK-CAMBIUM or PHELLOGEN is usually formed in the first season, soon after, or even before, the commencement of secondary growth. It may arise from the epidermis by tangential division of its cells. More usually, however, it is formed from the layer of cortex just below the epidermis, less commonly from a deeper layer of the cortex or from the pericycle. The last case is the rule for roots (Fig. 164 *B*, *k*). The meristem and all the products of its activity are known collectively as the PERIDERM. The cells cut off to the outer side become CORK-CELLS; those developed to the inner side become unsuberised cells with abundant chlorophyll, which round off and are added to the cortex. With the formation of the periderm the surface of the stem appears brown.

The cells formed on the inner side by the phellogen are termed collectively the PHELLODERM.

The cork-cambium is as a rule a typical initial cambium (cf. p. 44), at least when it forms both cork and phelloderm. An initial layer may, however, be wanting e.g. in many Monocotyledons; in this case the permanent cells from which the cork-cambium proceeds divide into a number of cells which become cork-cells, and the process is repeated in adjacent cells of the permanent tissue.

Periderm formation takes place at a later period in those plants in which the epidermis continues to expand for years; it is wanting only in the species of Mistletoe.

True cork is wanting in Cryptogams, even in the Pteridophytes. When protection is required its place may be taken by the impregnation of the cell-walls with a very resistant brown substance or by the addition of suberised lamellae to the walls, that is, the transformation of certain layers of cells into a cutis-tissue (94).

3. Formation of Bark.—All tissues external to the cork-cambium are cut off from supplies of water and food-materials and consequently die. The dead tissue, including the layer of periderm, is termed BARK. According to the depth at which the periderm is formed this may include only the epidermis or a larger or smaller proportion of the cortex. The first layer of cork-cambium in stems and roots usually soon ceases to be active; this does not happen in the Beech. A new layer of cork forms deeper in the stem, and its activity in turn comes to an end; another layer forms still more deeply as shown in Fig. 179. Ultimately the layers of cork are forming in secondary tissues in the living parenchyma of the zone of bast; thus in old stems all the living tissue external to the cambium is of secondary origin and the bark includes dead secondary tissues. The bark cannot follow the further increase in thickness of the stem or root, but is cast off in scales or torn by longitudinal fissures. It forms an even more complete protection than the cork against both loss of water and overheating.

Since in the formation of bark the more external and oldest parts of the bast are thus shed, the zone of bast remains relatively thin. Mechanical tissues can only be permanent constituents of the stem when formed internal to the cambial ring, *i.e.* in the wood.

If the layers of the secondary periderm constitute only limited areas of the circumference of the stem the bark will be thrown off in scales, as in the SCALY BARK of the Pine, Oak (Fig. 179), and Plane tree: if, on the contrary, the periderm layers form complete concentric rings, hollow cylinders of the cortical tissues are transformed into the so-called RINGED BARK, such as is found in the Grape-vine, Cherry, Clematis, and Honeysuckle.

When the bark peels off from the stem in layers this is not a purely mechanical result; it depends on an ABSCISS LAYER consisting of thin-walled cork-cells or phelloid cells (cf. p. 55) which are formed between the other layers of cork with thickened walls. These absciss layers are ruptured by the hygroscopic tensions set up in the bark. Bark which is not easily detached becomes cracked by the continued growth in thickness of the stem, and has then the furrowed appearance so characteristic of the majority of old tree-trunks.

The usual brown or red colour of bark, as in similarly coloured heart-wood, is occasioned by the presence of tannins, to the preservative qualities of which is due the great resistance of bark to the action of destructive agencies. The peculiar white colour of Birch-bark is caused by the presence of granules of betulin (birch-resin) in the cells.

Healing of Wounds (^{95}).—In the simplest cases among land-plants the wounded cells die and become brown and dry, while the walls of the underlying uninjured cells become impregnated with protective substances and sometimes also form suberised lamellae. In the case of larger wounds in the Phanerogams a cork-cambium forming WOUND-CORK develops below these altered cells much as in the case of leaf-scars (p. 115).

When young tissue is exposed by a wound, a formation of CALLUS usually takes place. All the living cells which abut on the wound grow out and divide, becoming closely approximated. In most cases a cork-cambium forms in the peripheral layers of the callus and gives rise to cork. In stems of Gymnosperms and Dicotyledons, wounds which extend into the wood become surrounded and finally covered over by an outgrowth of tissue arising from the exposed cambium. While the callus-tissue is still in process of gradually growing over the wounded surface, an outer protective covering of cork is developed ; at the same time a new cambium is formed within the callus by the differentiation of an inner layer of cells, continuous with the cambium of the stem. When the margins of the overgrowing callus-tissue ultimately meet and close together over the wound, the edges of its cambium unite and form a complete cambial layer, continuing the cambium of the stem over the surface of the wound. The wood formed by this new cambium never coalesces with the old wood which is brown and dead. Accordingly, marks cut deep enough to penetrate the wood are merely covered over by the new wood, and may afterwards be found within the stem. In like manner, the ends of severed branches may in time become so completely overgrown as to be concealed from view. As the wood produced over wounds differs in structure from normal wood, it has been distinguished as CALLUS-WOOD. It consists at first of almost isodiametrical cells, which are, however, eventually followed by more elongated cell-forms. In the Cherry instead of normal wood-elements nests of thin-walled parenchymatous cells which undergo gummosis (p. 37) are produced on wounding the cambium.

2. Adaptations of the Cormus to its Mode of Life and to the Environment (^{96})

The form and structure of the cormus are closely connected with its mode of life, which in turn depends on the environment. Practically all plants thus appear ADAPTED to the environments in which they are usually found. The uniform physiognomy exhibited by the plants of any locality, as well as the differences in the physiognomy of the vegetation in localities which differ in climate, depend upon this. The vegetative organs are therefore not typically constructed in all cormophytes, but are frequently altered or METAMORPHOSED in a variety of ways. Very careful developmental or anatomical investigation may be required to show that the variously-constructed organs of many cormophytes are derived by the metamorphosis of the three primary organs, root, stem, and leaf, and to ascertain with which of these any particular structure is really homologous. The external form and the functional activity of mature organs may be very misleading. One organ may assume the form and functions of another, *e.g.* a stem resembling a leaf; different primary organs may take on the same forms in relation to performing the same functions and thus be analogous but not homologous. As a rule, however, when all the characters of an altered organ are taken into consideration, some will leave no doubt as to its morphological origin.

The form of a plant and of its parts is determined in the first place by its mode of nutrition. Thus there are striking and important morphological differences between cormophytes which require only inorganic food materials (AUTOTROPHIC PLANTS) and those which require organic food (HETEROTROPHIC PLANTS).

A. Autotrophic Cormophytes

The green plants are structurally adapted to autotrophic life. The typical features of the construction of autotrophic cormophytes have been described above. The green cormophytes may exhibit considerable variety among themselves, for their structure is adapted to the different features of the environments in which they occur.

Among the numerous factors in the differing external conditions, WATER and LIGHT have by far the greatest influence on the form of green plants. This is evident, for the plant can only carry on its life when sufficient water is available, and only when there is sufficient light can it construct organic substance from inorganic food materials and thus be autotrophic.

(a) Adaptations to the Humidity of the Environment

1. Water Plants. Hydrophytes (97).—Special peculiarities in structure are found in plants which live in water (HYDROMORPHY). These can absorb both water and nutrient salts and also the necessary gases (carbon-dioxide and oxygen) from the water by the whole surface of their stems and leaves. In considering the conditions of life in water it is essential to know the amounts of various gases which can be dissolved and to contrast this with their presence in the atmosphere. One litre of air contains about 210 c.cm. oxygen and 0·3 c.cm. of carbon-dioxide. In one litre of water at 20° C., on the other hand, there can be dissolved only about 6 c.cm. oxygen, but 0·3 c.cm. carbon-dioxide. There is thus available for the submerged plant as much carbon-dioxide, or even somewhat more if we take account of the effect of carbonates in solution in the water. There is, however, little oxygen, especially in the case of still water, since the diffusion of this gas in water is very slow.

The thin walls of the epidermal cells of the shoot have a very thin cuticle that offers little hindrance to the entrance of water and dissolved salts, especially in the case of the leaves ([98]). The large surface exposed by the fine subdivision of the lamina of the submerged leaves (*Batrachium*, Fig. 135, *Utricularia, Myriophyllum, Ceratophyllum*) stands in relation to the slowness of the diffusion of gases in water; floating and aerial leaves of water-plants, on the other hand, are typically formed (heterophylly, cf. p. 113). As regards their anatomy the submerged leaves are characterised by the absence of stomata, and usually of hairs from the epidermis, the cells of which contain chlorophyll; the mesophyll has large intercellular spaces, and consists of uniform parenchyma, not showing the distinction of palisade and spongy tissue. The leaves in transverse section thus appear bilaterally symmetrical (Fig. 180). The feeble development of water-conducting elements in the stems and leaves, the absence of secondary thickening, and the absence of roots (*Utricularia, Ceratophyllum, Wolffia*), are related to the absence of transpiration, and of active transport of water. The support afforded by the surrounding water renders mechanical tissues unnecessary; the pulling forces exerted in quickly-flowing water are met by the central position of the vascular bundle.

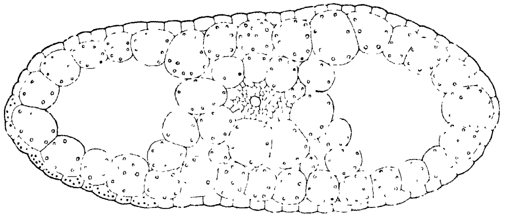

FIG. 180.—Transverse section of the leaf of *Zannichellia palustris*. (× 146. After SCHENCK.)

A feeble movement of water through the plant which is connected with the excretion of water from openings at the tips of the leaves (cf. p. 110) can be demonstrated in many submerged water-plants.

The great development of the intercellular spaces is a striking feature of almost all aquatic and marsh plants. They are wide, and form a regular system of air-filled chambers and passages, which are separated by parenchymatous partitions, usually only one cell thick: this is the case, for example, in the stems of *Papyrus*, *Potamogeton*, etc., in the petioles of the Nymphaeaceae, and in the roots of *Jussieua*. Such tissue is termed AERENCHYMA. Since its wide air-passages serve for the storage of air, and allow of ready diffusion of gases within the body of the plant, the rapid transport of oxygen from the assimilating green organs to the colourless organs greatly facilitates respiration.

In some swamp-plants, the subterranean organs of which are in swampy soil with little oxygen, special organs are concerned with obtaining this gas; respiratory roots (PNEUMATOPHORES, Fig. 181) grow erect from the muddy soil, obtaining oxygen from the air by lenticel-like PNEUMATHODES, and conducting it by the aerenchyma to the subterranean parts. Such plants are found among the Palms and in the Mangroves of tropical coasts, some of which are also anchored to the mud by a system of aerial stilt-roots springing from the shoots (Fig. 182) (96).

2. Land-Plants.—These usually obtain water and nutrient salts from the soil, and oxygen and carbon-dioxide from the atmosphere; their aerial shoots give off water in the form of vapour in the process of transpiration.

A few plants of very moist habitats, especially the Hymenophyllaceae of tropical forests, which can absorb water by the general surface, form an exception. Some of them develop no roots but have a system of water-absorbing hairs on their stems or leaves which considerably increase the absorbent surface.

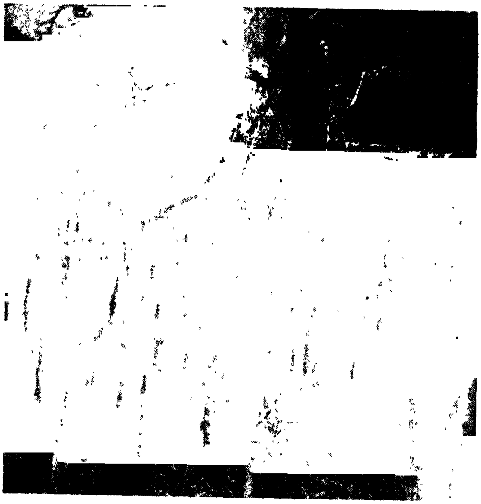

FIG. 181.—Respiratory roots of *Sonneratia alba*. (After JOH. SCHMIDT.)

The construction of land plants differs according to their occurrence in constantly moist localities, dry localities or climates, or intermittently moist climates.

(a) Adaptations to constantly moist Habitats. Hygrophytes (99).—Terrestrial plants which inhabit situations in which the atmosphere is permanently moist, such as many shade plants, are spoken of as HYGROPHILOUS or HYGROPHYTES. Like water-plants they have no need of arrangements to diminish transpiration, but, on the contrary, require to facilitate the giving off of water from the aerial shoots (HYGROMORPHY). Only in this way can a sufficiently active movement of water from the roots in the soil to the organs above ground be ensured to supply the requisite quantity of nutrient salts. When the air is too dry they soon wilt and may perish. Many hygrophytes, especially those that inhabit the moistest situations (*e.g.* moist tropical forests), resemble water-plants in form and structure.

Hygrophytes have expanded, thin, leaf-blades of delicate texture; these have no covering of dead hairs, but are either smooth or have a velvety upper surface, due to the presence of numerous living hairs or papillae. The outer walls of the epidermal cells, which contain chloroplasts, are very thin and covered by a delicate cuticle. The not very numerous stomata are not sunken but frequently are even raised above the general level of the epidermis. The large-celled mesophyll has very large intercellular spaces. The process of assimilation in the weak illumination of the shaded habitats requires to be facilitated in these plants by their hygromorphy. Many hygrophytes have, in their hydathodes, means of giving off liquid water (Fig. 238) when transpiration in the moist air is almost stopped. The water may be actively secreted by glandular hairs or passively pressed out from the vascular bundles through water-stomata (Fig 130).

In correspondence with their constantly moist and shaded habitats and reduced transpiration the root-system and the water-conducting vascular tissues of hygrophytes are usually poorly developed.

(b) Adaptations to physiologically dry Habitats or to dry Climates. Xerophytes ($^{96, 100}$).

Plants, the shoots of which are exposed to dry air while they have difficulty in obtaining an adequate or sufficiently rapid supply of water to make good the loss in transpiration, require arrangements to diminish the latter process. The ordinary limitation of transpiration by closure of the stomata is not sufficient in the case of plants of exceptionally dry habitats or climates. Only a few cormophytes can withstand drying up, as do many Lichens and Bryophyta (cf. p. 205), and most of them die when wilting is carried far.

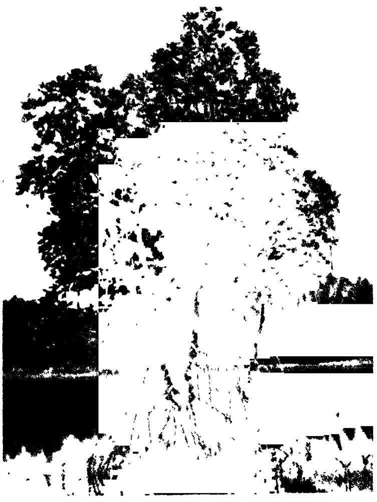

FIG. 182.—Stilt-roots in *Rhizophora mucronata* in the Malay Archipelago. (After KARSTEN.)

Plants with such arrangements to diminish the loss of water are termed XEROPHILOUS or XEROPHYTES. They are recognisable by their general habit. The morphological peculiarities which are involved in arrangements to diminish transpiration are referred to collectively as the xerophytic structure (XEROMORPHY). Desert plants, the plants of dry rocks and many epiphytes (cf. p. 173) are naturally extreme xerophytes. There are also xerophytes without marked xeromorphy. These are able to obtain water from relatively dry soil owing to the high absorbent power resulting from a concentrated cell-sap.

Both morphological and anatomical arrangements are concerned in diminishing transpiration. Some of these adaptations may at the same time be protective against strong insolation or overheating.

The following are **anatomical** features which serve to diminish transpiration: thick cutinised epidermal cell-walls and cuticle; reflection of light from the cuticle; mucilaginous epidermal cells; formation of waxy and resinous coatings; accumulation of calcium carbonate; in the case of stems and roots, layers of cork; reduction in the number of stomata; narrowing of the stomata and their occlusion by resin or wax; sinking of the stomata below the general level of the epidermis, either singly (Fig. 183) or in numbers in special flask-shaped depressions of the under side of the leaf (*e.g.* Oleander), or the over-arching of the stomata by adjoining cells so that they come to be situated in cavities protected from the wind. Hairs, whether woolly, stellate, or scaly, which early become filled with air and give the plants a whitish or grey appearance (Edelweiss, Australian Proteaceae, Olive), may serve as a protection against the sun's rays. On the other hand, evergreen leaves may be small, leathery, and relatively poor in sap (*e.g.* sclerophyllous evergreen plants of the Mediterranean region, such as the Olive and Myrtle). The small size of the intercellular spaces in the mesophyll is characteristic of the leaves of well-marked sclerophylls (Fig. 186); there is often no spongy tissue, but frequently several layers of palisade-cells beneath both upper and lower epidermis so that the structure of the leaf becomes bilaterally symmetrical.

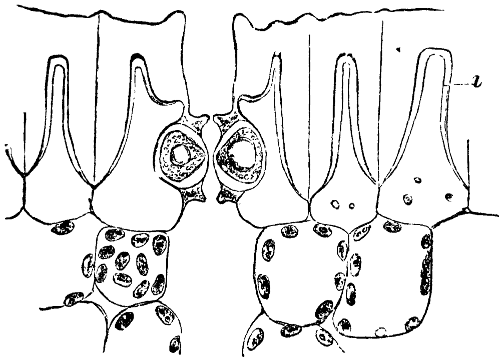

FIG. 183.—Transverse section of the epidermis of *Aloe nigricans*. *i*. Inner, uncutinised thickening layer. (× 240. After STRASBURGER.)

By sinking of the stomata or by a covering of dead hairs spaces of quiet air saturated with water-vapour are obtained. The effect of this is to diminish the evaporation from the stomata.

In not a few otherwise xeromorphous xerophytes the number of stomata per sq. cm. of the leaf surface is especially large. This is also found in some sun-leaves. This peculiarity must be advantageous for assimilation while the stomata remain more or less open in air that is not too dry.

These anatomical arrangements are usually associated with **morphological** peculiarities of the **external form.**

Many xerophytes with small leaves have the branches crowded together to form a dense cushion (*e.g.* many Alpine plants, Fig. 184); not only is transpiration checked by this, but a protection against too strong insolation is obtained.

A very effective protection against transpiration and light is obtained by the leaf-surface being placed vertically (Australian Acacias and Myrtaceae); this is often associated with a reduction of the lamina and a flattening of the petiole (PHYLLODES, Figs. 136, 185). Such leaves avoid more or less completely the rays of the sun when this is at its highest, and excessive heating and transpiration are thus prevented.

A similar position of the leaves is met with in some of our native plants such as *Lactuca scariola*, the Compass Plant in which all the leaves stand vertically and in the direction of north and south

The most important and most frequent means of protection against excessive transpiration is by the reduction of the transpiring surface. This is effected by the dwarfing of the plant (NANISM) by diminished branching, by reduction in the number of leaves, and lastly by reduction of the shoots or leaf-blades. The free surface of the leaf is reduced in the grasses of exposed situations and in certain Ericaceae by the inrolling of the surface (Fig. 187). In the Genisteae, Cupressaceae, and some New Zealand species of *Veronica* (cf. also Fig. 188), it is effected by reduction of the lamina, which is completely lost in Cactaceae, in some tree-like species of *Euphorbia*, and in some Asclepiadaceae.

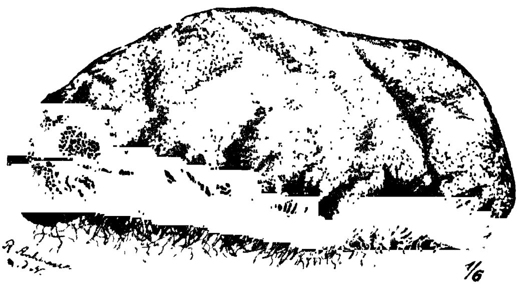

FIG. 184.—*Raoulia mammillaria* from New Zealand, showing the cushion-like shape. (From SCHIMPER'S *Plant-Geography*.)

With the reduction in the leaf-surface the assimilation of carbon is also diminished, and a compensatory development of chlorophyll-containing parenchyma takes place in the stems of such plants. The twigs of the Broom (*Sarothamnus scoparius*), which bear only occasional leaves that are soon shed, are elongated and green (SCLEROCAULOUS PLANTS). A striking modification is exhibited by shoots which only develop reduced leaves, while the stems become flat and leaf-like and assume the functions of leaves. Such leaf-like shoots are called CLADODES or PHYLLOCLADES (Figs. 189. 190), those flattened shoots which have limited growth and specially leaf-like appearance being termed phylloclades, and other flattened axes cladodes. An instructive example of such formations is furnished by *Ruscus aculeatus* (Fig. 189), a small shrub of the Mediterranean region whose stems bear in the axils of their scale-like leaves (*f*) broad sharp-pointed phylloclades (*cl*) which have altogether the appearance of leaves. The flowers arise from the upper surface of these phylloclades, in the axils of scale-leaves. This affords a good example of the analogy between organs. The appearance and functions of the phylloclades are those of leaves, but the morphological features mentioned above show that they are shoots. A leaf-like flattening of the massive stems, which thus form cladodes, is met with in the well-known Opuntias (Fig. 190), the bases of the branches remaining narrow.

Special interest attaches to some xerophytes in which the stems as well as the leaves are reduced. Thus in the epiphytic orchid *Taeniophyllum* (Fig. 191) the flattened green roots represent the vegetative organs and carry on the functions of the leaves.

The great development of sclerenchyma in the shoots of many xerophytes not only contributes to the rigidity of the plant, but is associated with the development of THORNS. Thus spiny shoots, though not lacking in plants of our own climate that are not xeromorphic, are characteristic of many xerophytes of deserts and steppes. The thorns are lignified and rigid pointed structures that may either be unbranched or branched. They originate by the modification of leaves or parts of leaves (LEAF-THORNS), of shoots (SHOOT-THORNS), or less commonly of roots (ROOT-THORNS). In the Barberry (*Berberis vulgaris*) the leaves borne on the main shoots are transformed into thorns which are usually tri-radiate, while the lateral branches

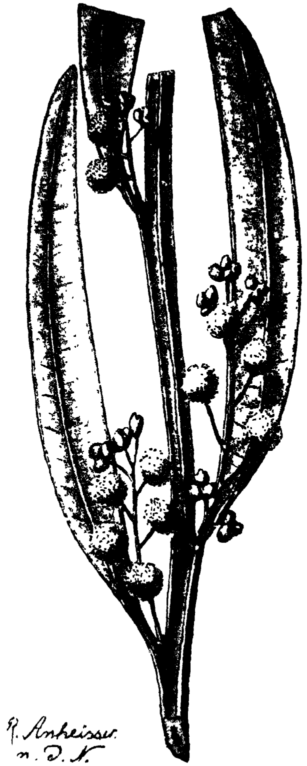
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FIG. 185.—*Acacia marginata*, with vertically-placed phyllodes. (From SCHIMPER'S *Plant-Geography*.)

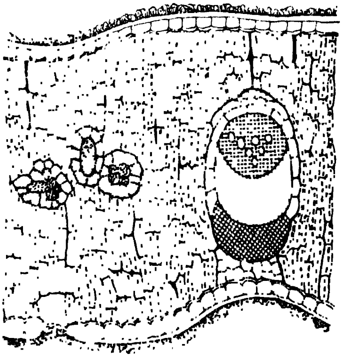


FIG. 186.—Transverse section of the leaf of *Capparis spinosa*, var. *aegyptiaca*. (× 40. SCHIMPER, after VOLKENS.)

bearing the foliage leaves stand in the axils of these thorns. In the Cactaceae also (Fig. 190) the thorns arise from leaf-primordia. In *Robinia* (Fig. 192, cf. also *Accacia*, Fig. 699), and in the succulent species of *Euphorbia*, the two stipules of each leaf form thorns. Shoot-thorns are found in *Prunus spinosa*, *Crataegus oxycantha*, and *Gleditschia* (Fig. 193).

In *Colletia cruciata* all the shoots are flattened and spiny, so that, in addition to serving as protective structures, they perform the duties of the leaves which are soon lost. The plant is an American shrub belonging to the Rhamnaceae and grows in dry sunny situations. Root-thorns occur on the stems of some Palms e.g. *Acanthorrhiza*) and in *Myrmecodia* among Dicotyledons.

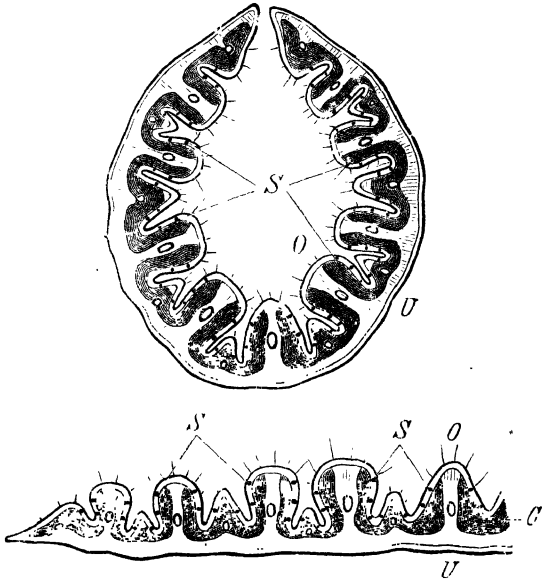


FIG. 187.—Transverse sections of the leaf of *Stipa capillata* (Gramineae). The leaf above in the closed state, the half leaf below expanded. *U*, lower surface, without stomata; *O*, upper surface, with stomata (*S*); *C*, chlorophyllous mesophyll. (× 30. After KERNER VON MARILAUN.)

Many xerophytes not merely strictly control the giving off of water in transpiration, but, when it is obtainable, store water in special water-storage tissues against periods of need (cf. p. 46). In some cases the epidermal cells attain a large size or they may be divided parallel to the upper surface and give rise to a many-layered water-tissue (various Piperaceae, Begoniaceae, species of *Ficus*, *Tradescantia*). The water-storage tissue often has a more central position, and when largely developed gives the character of succulent plants. In certain Umbelliferae, Cucurbitaceae, Compositae Asclepiadaceae, and in species of *Pelargonium* and *Oxalis* of the steppes and deserts the roots are transformed for water-storage. Leaf-succulents are more common (*e.g.* *Sedum*, *Sempervivum*, *Agave*, *Aloe*, (Fig. 833) *Mesembryanthemum*), while examples of stem-succulents are afforded by the Cactaceae, species of *Euphorbia*, *Stapelia*, and other Asclepiadaceae (Figs. 190, 194) and *Kleinia* among the Compositae. The columnar or spherical

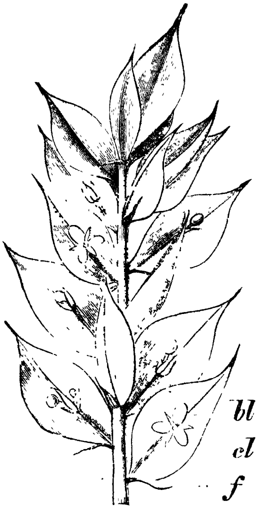


FIG. 189.—Twig of *Ruscus aculeatus* (Liliaceae). *f*, Leaf; *cl*, phylloclade; *bl*, flower. (Nat. size. After SCHENCK.)

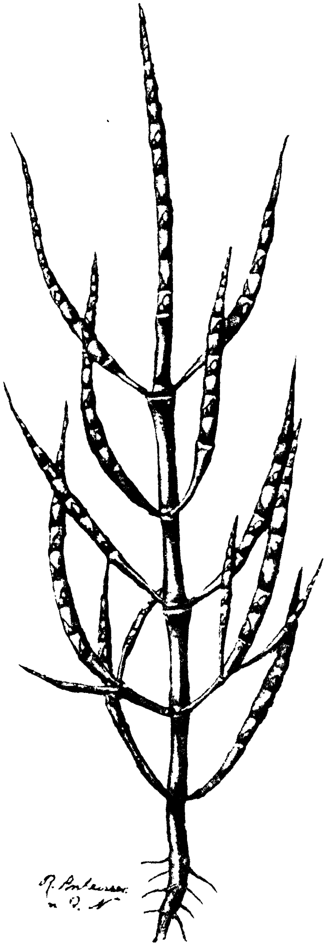


FIG. 188.—*Salicornia herbacea* (Chenopodiaceae), a characteristic halophyte. (From SCHIMPER'S *Plant-Geography*.)

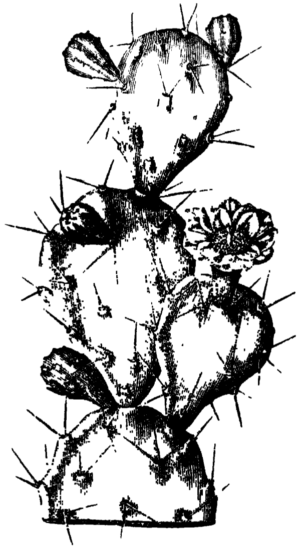


FIG. 190.—*Opuntia monacantha*, Haw., showing flower and fruit. (½ nat. size. After SCHUMANN.)

Cactaceae are especially characteristic of arid regions in the new world, while Euphorbias and Asclepiadaceae of similar habit take their place in the eastern hemisphere (Fig. 194 *a-c*). The "cactus-form" is evidently very advantageous for xerophytes especially for those that have to succeed in very dry situations. Similarity in the mode of life has thus brought about a corresponding form in widely distinct plants. This phenomenon of CONVERGENCE OF CHARACTERS is not infrequent. In extreme cases the form of the stem or the leaf of succulent plants may approach that of a sphere; this, for a given volume, exposes the minimum surface and is thus advantageous in diminishing transpiration. NOLL has estimated that the loss of water from a spherical Cactus is 600 times less than from an equally heavy plant of *Aristolochia sipho* with its much greater surface. Such succulent stems are really tuberous storage organs for water.

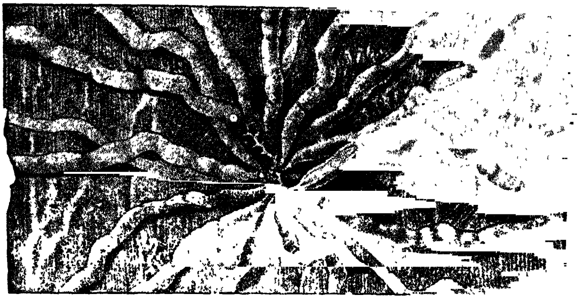


FIG. 191.—*Taeniophyllum Zollingeri.* A xerophytic orchid without leaf or stem but with green flattened roots. (Nat. size. From SCHIMPER'S *Plant-Geography*, after WIESNER.)

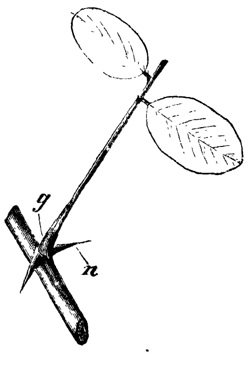


FIG. 192.—Part of stem and compound leaf of *Robinia Pseudacacia*. *n*, Stipules modified into thorns; *g*, pulvinus. (½ nat. size. After SCHENCK.)

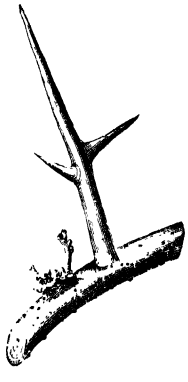


FIG. 193.—Stem-thorn of *Gleditschia triacanthos*. (½ nat. size. After SCHENCK.)

(c) Adaptations to periodically moist Climates. Tropophytes (96). In some moist and warm regions the climate remains almost equally favourable to the growth of plants throughout the year. Wherever, however, there is a marked periodicity in the climate, with an alternation between a period favourable to the growth of plants and a more or less injurious season, a corresponding

PERIODICITY is found in the vital processes of the plants. The resting period may be brought about either by dryness or by the cold of a winter season. Many of the plants living under such a climate show differences in structure as compared with those of uniformly moist tropical regions. Only those forms will succeed that can endure the unfavourable period in one way or another. The main danger when a cold winter alternates with a summer period lies in death from lack of water during the physiologically-dry cold period. This danger does not threaten extreme xerophytes since they are suited to dry habitats in the favourable period. It is otherwise with plants that are not xeromorphic. The majority of our native cormophytic plants show protective arrangements against an unfavourable season. In the favourable period they resemble hygrophytes in not requiring any special protection against excessive transpiration, but they behave as extreme xerophytes during the unfavourable period. Such plants are spoken of as tropophytes.

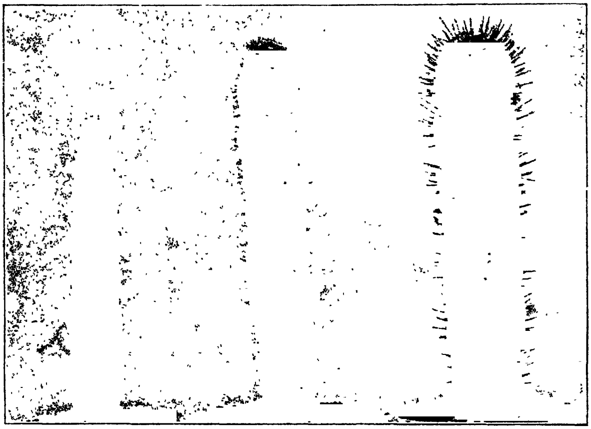


FIG. 194.—Plants with succulent stems. *a*, *Stapelia grandiflora*; *b*, *Cereus Pringlei*; *c*, *Euphorbia erosa*. ($\frac{1}{3}$ nat. size.)

The plants of periodically moist climates may be perennial woody plants (trees and shrubs), perennial herbaceous plants, and annual herbs.

It is especially the leaves as the organs of transpiration that are exposed to risk during dry periods. Thus the shedding of the hygromorphic leaves before the unfavourable period in the case of deciduous trees or the dying down of the leafy shoots in many herbaceous plants is readily understood. A few evergreen plants with xeromorphous leaves (*e.g.* the Conifers and *Ilex*) appear as exceptions to this. Further, the embryonic tissue, from which the lost parts will be replaced at the commencement of the favourable season, may require to be specially protected from the risk of desiccation. This is effected in a variety of ways.

1. The **woody plants** of periodically moist climates protect the growing points within WINTER BUDS (Fig. 195) during the dry or winter period.

Such buds are protected by the BUD-SCALES which are in close contact. These may be derived from entire primordial leaves that remain unsegmented but more commonly are formed from the enlarged and modified leaf-base. The upper portion of the leaf may scarcely develop or may be recognisable at the tip of the bud-scale in a more or less reduced condition. Thus in an opening bud of the Horse Chestnut (*Aesculus hippocastanum*) in the spring the small leaf-blade can be clearly seen in the case of the inner bud-scales, while it is scarcely visible on the outer scales. In other cases (*e.g.* in the Oak) the bud-scales arise from stipules and thus also belong to the leaf-base. The base of a subtending leaf may remain and cover the axillary bud after the rest of the leaf is shed; in *Robinia* such a leaf-base provides the entire protection for the winter-bud.

Bud-scales are thick, leathery, and hard, and usually brown in colour. They are rendered even more effective in protecting the buds from desiccation by corky or hairy coverings, by excretions of resin, gum, or mucilage, and by the enclosure of air between the scales. Resin, etc., are usually secreted by peculiar, stalked, glandular hairs or COLLETERS (cf. Fig. 53); in the case of the winter buds of many trees (*e.g.* the Horse Chestnut) a mixture of gum and resin is thus secreted and, becoming free on the bursting of the cuticle, flows between the scales, sticking them together. When the buds open in the spring the bud-scales as a rule are shed. The internodes between them being very short, the scales leave closely crowded scars on the shoots by the help of which the growth of successive years can be recognised.

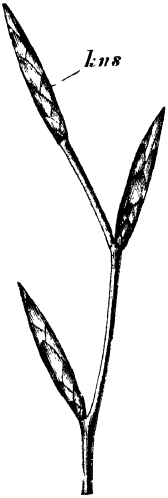


FIG. 195.—Winter buds of the Beech (*Fagus sylvatica*). *kns*, Bud-scales. (Nat. size. After SCHENCK.)

2. The **perennial herbs** sacrifice not only the leaves but whole leafy shoots with their buds, so far as these project in the air and are exposed to the danger of drying. The buds that persist through the winter may be just above the surface of the soil but protected by fallen leaves or by snow, or they are subterranean (geophytes) and more effectively protected both against desiccation and frost by the surrounding earth.

When the persisting buds are above ground they may be borne on creeping surface shoots (*e.g. Saxifraga, Stellaria holostea, Thymus*, etc.), or on subterranean shoots or rhizomes, as in the perennial rosette-plants (*Bellis, Taraxacum, Primula*), and in biennials which pass the winter with a rosette of leaves (*e.g. Verbascum*, *Digitalis*, etc.). Here also, as in the case of geophytes, subterranean storage organs may occur.

In the GEOPHYTES (101) or herbs with subterranean buds which persist through the winter, the parts which bear the buds have a construction corresponding to their life in the soil. They may be metamorphosed shoots (RHIZOMES, TUBERS, BULBS), or metamorphosed roots ROOT-TUBERS). The buds that form new shoots in the spring require a supply of food-materials, especially when they are placed some distance below the surface. These food-materials were constructed in the preceding favourable season before the aerial shoots died down. The subterranean organs, formed largely of storage parenchyma, are naturally thick or swollen, to allow of the accumulation of reserve-materials. Such storage organs are utilised by many animals and by man as a source of food. They become gradually depleted at the commencement of the period favourable for vegetation, and then (except in the case of many rhizomes) perish and are replaced.

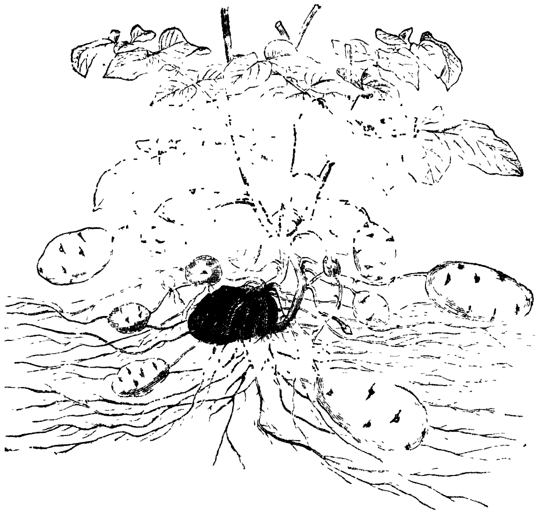


FIG. 196.—Part of a growing Potato-plant, *Solanum tuberosum*. The whole plant has been developed from the dark-coloured tuber in the centre. (⅓ nat. size. After SCHENCK.)

(*a*) Root-stocks or RHIZOMES and STEM-TUBERS are colourless subterranean shoots, the former being thick or relatively thin with shorter or longer internodes (Figs. 121, 139), while the latter (*e.g.* the Potato-tuber, Fig. 196) are greatly thickened. The leaves, as is the rule in subterranean shoots, are developed as scales. The reserve-materials are stored in the stem, which is on this account usually swollen. By the presence of scale-leaves, with their axillary buds, the absence of a root-cap and the internal structure, a rhizome or tuber can be distinguished from a root.

While all transitions between rhizomes and shoot-tubers exist, roots are usually absent from the latter, while the rhizomes, which may grow horizontally, obliquely, or vertically, and be branched or unbranched, as a rule bear roots.

In Fig. 139 is shown the rhizome of Solomon's Seal (*Polygonatum multiflorum*), which has been already referred to as an example of a sympodium. At *c*, *d*, and *e* are seen the scars of the aerial shoots of the three preceding years; at *b* may be seen the base of the stem growing at the time the rhizome was taken from the ground, while at *a* is shown the bud of the next year's aerial growth.

The tubers of the Potato, of *Colchicum autumnale*, and *Crocus sativus*, are examples of stem-tubers. The tubers of the Potato (Fig. 196) are subterranean shoots with swollen axes and reduced leaves. They are formed from the ends of branched underground shoots or runners (STOLONS), and thus develop at a little distance from the parent-plant. The so-called eyes on the outside of a potato, from which the next year's growth arises, are in reality axillary buds, but the scales which represent their subtending leaves can only be distinguished on very young tubers. The parent-plant dies after the formation of the tubers, and the reserve-food stored in the tubers nourishes the shoots which afterwards develop from the eyes.

In the Autumn Crocus (Fig. 830), new tubers arise from axillary buds near the base of the modified shoot, but in the Saffron (Fig. 839), from buds near the apex. In consequence of this, in the one case the new tubers appear to grow out of the side, and in the other to spring from the top of the old tubers.

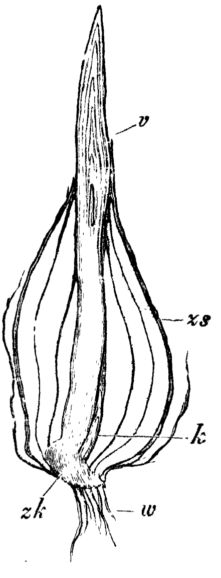


FIG. 197. — Longitudinal section of Tulip bulb, *Tulipa Gesneriana*. *zk*, Modified stem; *zs*, scale-leaves; *v*, terminal bud; *k*, rudiment of a young bulb; *w*, roots. (Nat. size. After SCHENCK.)

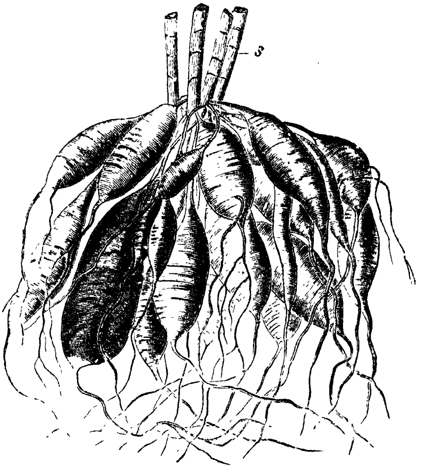


FIG. 198.—Root-tubers of *Dahlia variabilis*. *s*, The lower portions of the cut stems. ($\frac{1}{6}$ nat. size. After SCHENCK.)

The Radish is also a tuberous stem, although only a portion of a single internode, the hypocotyl of the seedling, is involved in the swelling. The uppermost portion of the main root also contributes to this.

The Kohl rabi has an above-ground tuberous stem derived from a number of internodes of the shoots and rich in stored reserve-materials.

(*b*) BULBS (*e.g.* Onion, Tulip, Hyacinth) also belong to the class of subterranean metamorphosed shoots. They represent a shortened shoot with a flattened discoid stem (Fig. 197 *zk*), the fleshy thickened scale leaves (*zs*) of which are filled with reserve food-material. The aerial shoot of a bulb develops from its axis, while new bulbs are formed from buds (*k*) in the axils of the scale-leaves.

(*c*) Other herbaceous perennials of periodically moist climates (*e.g.* the Dahlia and many Orchids) form ROOT-TUBERS (Figs. 198, 199). They resemble the stem-tubers, though their true nature can be recognised by the presence of a root-cap, the absence of leaves, and the internal structure. Tuberous main roots are found in the Carrot and the Beet, both of which are biennial plants.

The morphology of the tubers of the Orchidaceae is peculiar; they are ovate (Fig. 199, cf. Figs. 857, 861) or palmately divided (*Orchis latifolia*, Fig. 858). They are, to a great extent, made up of a fleshy swollen root terminating above in a shoot-bud. In the adjoining figure (Fig. 199) both an old (*t′*) and a young tuber (*t″*) are represented still united together. The older tuber has produced its flowering shoot (*b*), and has begun to shrivel; a bud, formed at the base of the shoot, in the axil of a scale-leaf (*s*), has already developed an adventitious root which has given rise to the younger tuber. Roots of ordinary form arise from the base of the stem above the tuber.

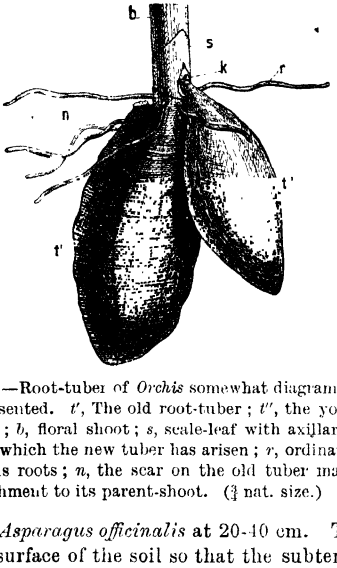


FIG. 199.—Root-tuber of *Orchis* somewhat diagrammatically represented. *t′*, The old root-tuber; *t″*, the young root-tuber; *b*, floral shoot; *s*, scale-leaf with axillary bud, *k*, from which the new tuber has arisen; *r*, ordinary adventitious roots; *n*, the scar on the old tuber marking its attachment to its parent-shoot. (¾ nat. size.)

Many bulbs, tubers, and rhizomes occur at a SPECIFIC DEPTH, which may, however, vary with the nature of the soil. Thus the rhizome of *Paris* is placed at a depth of 2-5 cm., that of *Arum* at 6-12 cm., of *Colchicum* at 10-16 cm., and of *Asparagus officinalis* at 20-40 cm. The seeds of these plants germinate close to the surface of the soil so that the subterranean shoots of the young plants must penetrate more and more deeply into the earth. This may be effected by the movements of growth of the stem (cf. p. 346) or by contractile roots. Thus in *Lilium* (Fig. 200) all the roots are highly contractile; this is best seen in Fig. 200, 3, where the two lowest roots have contracted strongly and so altered the position of the bulb that the higher roots appear curved near their attachment. When the bulb has reached the proper depth it is only drawn down each year to compensate for the onward growth of the growing point. In other cases all the roots are not contractile (*Arum*), or only one or a few contractile roots are developed (*Crocus*, *Gladiolus*). While the above examples are of lateral roots a similar result may be brought about by the main root. Thus in some rosette-plants the main root continues to contract as secondary growth proceeds, so that the growing point of the shoot is drawn down each year as much as it is raised by its own growth, and the rosette of leaves remains pressed against the surface of the soil (*e.g. Gentiana lutea*).

3. **Annual herbs** do not retain their vegetative organs during the unfavourable season, which they pass safely in the form of dry seeds within which the reserve-materials are stored.

The more uniformly favourable for vegetation the climate is throughout the year (as in the moist tropical regions) the more do evergreen woody plants preponderate, though evergreen perennial herbs are also present. On the other hand, as the periodicity in the climate becomes more extreme, as in regions with a long dry period or in climates with severe winters, the percentage of deciduous tropophytes with marked protective arrangements increases, while annual plants and geophytes preponderate among the herbs. Annual plants become rare in regions where the growing season is very short and cold as in the case of arctic and alpine floras.

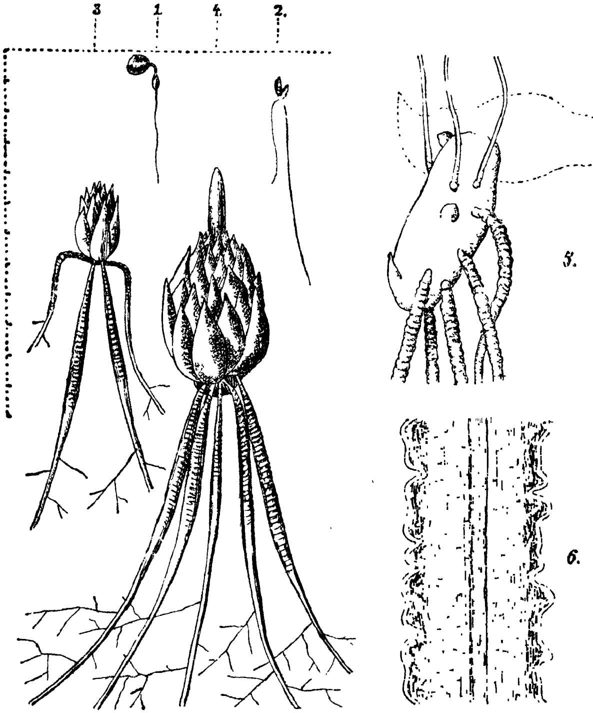


FIG. 200.—*1–4*, Germination of *Lilium martagon* (reduced). The horizontal line marks the surface of the soil; the vertical line is graduated in centimetres. *1*, Seedling attached to seed; *2*, plant at end of the second year; *3*, young plant still descending in the soil; *4*, full-grown plant at its normal depth. *5*, *Colchicum autumnale* (somewhat reduced). The original position of the tuber, which has been altered by the contraction of the roots, is shown by the dotted outline. *6*, Contracted root of *Lilium*. (× 6. After RIMBACH.)

(b) Adaptations for obtaining Light (96)

In the luxuriant vegetation produced under favourable climatic conditions plants of large or gigantic size are met with. The primeval tropical forest is composed of such large trees (cf. also p. 133), beneath the shade of which larger and smaller evergreen shrubs and evergreen herbaceous plants live. The direct sunlight is in large part intercepted by the foliage of the upper strata of this vegetation and does not reach the smaller plants.

In the struggle for light and space two groups of cormophytes of characteristic construction have emerged, in addition to trees and shrubs. These are the CLIMBING PLANTS or LIANES and the EPIPHYTES. They are specially characteristic of the tropics, though also represented in our native flora.

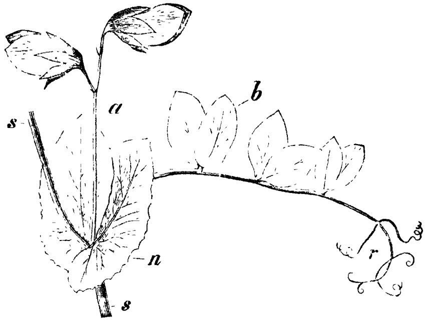


FIG. 201.—Portion of stem and leaf of the common Pea, *Pisum sativum*. *s*, Stem; *n*, stipules; *b*, leaflets of the compound leaf; *r*, leaflets modified as tendrils; *a*, floral shoot. (½ nat. size. After SCHENCK.)

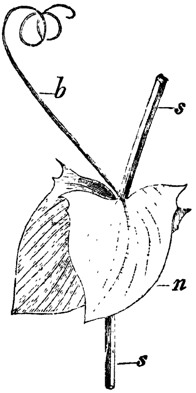


FIG. 202.—*Lathyrus Aphaca.* *s*, Stem; *n*, stipules; *b*, leaf-tendril. (½ nat. size. After SCHENCK.)

1. Lianes or Climbing Plants (102).—These are able without great expenditure of material in the construction of columnar stems to raise their foliage above the shade of the forest and obtain stronger light. Their slender stems climb by the help of the shoots, trunks, and branches of other plants. It is the rope-like stems of lianes that render many parts of the tropical jungle almost impenetrable.

Climbing is effected in a number of different ways. Some plants SCRAMBLE by means of hooked lateral shoots, by hairs and prickles, by a combination of these or by means of thorns (*e.g. Galium aparine*, Roses, *Solanum dulcamara*); others climb by means of roots (ROOT-CLIMBERS, *e.g.* Ivy, many Araceae, Fig. 826), or by twining stems (TWINING PLANTS, *e.g.* Hop, Scarlet Runner Bean); in others tendrils are developed as special organs of attachment (TENDRIL-CLIMBERS).

Tendrils are slender, cylindrical, branched or unbranched organs; they are irritable to contact (cf. p. 356), and thus able to encircle supports to which they attach the plant. They may be METAMORPHOSED SHOOTS (stem-tendrils) as in the Vine, the Wild Vine (Fig. 203), and the Passion-flower. In other cases they are TRANSFORMED LEAVES as in the Gourd, the Cucumber, and *Lathyrus aphaca* (Fig. 202); in the last example the functions of the leaf-blade, which has become the tendril, have been assumed by the expanded stipules. In the Pea (Fig. 201) and many other cases the uppermost leaflets of the pinnate leaf form a branched tendril.

In some forms of the Wild Vine *Parthenocissus* (Fig. 203) the branched tendrils bear attaching discs at their tips and can thus fasten the plant to flat surfaces.

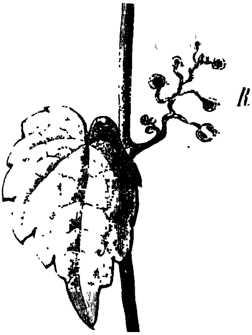


FIG. 203.—*Parthenocissus tricuspidata*. *R*, Stem-tendrils. (¾ nat. size. After NOLL.)

The great width of the vessels and sieve-tubes is characteristic of almost all lianes. In tropical climbers anomalous secondary growth (102) is frequently met with, resulting in a subdivided, woody mass that renders the long, rope-like stems capable of withstanding bending and twisting. A very peculiar structure is exhibited by many lianes of the Bignoniaceae, the wood of which is cleft by radially-projecting masses of bast (Fig. 205). The primary stem of the Bignoniaceae shows the ordinary circular arrangement of the vascular bundles. Wood and bast are at first produced from the cambium ring in the usual manner, and an inner, normal cylinder of AXIAL wood is formed. The cambium ring, after performing for a time its normal functions, begins, at certain points, to give off internally only a very small quantity of wood, and externally a correspondingly large amount of bast. As a result of this, deep wedges of irregularly-widening bast project into the outer so-called PERIAXIAL WOOD (Fig. 205). The originally complete cambium becomes thereby broken into longitudinal bands, which are broader in front of the projecting wood than at the apices of the bast-wedges. As the periaxial wood is always developed from the inside and the wedges of bast from the outside of their respective cambium bands, they extend past each other without forming any lateral connection. Several woody cylinders are found in a number of tropical lianes belonging to *Serjania* (Fig. 204) and *Paullinia*, which are genera of the Sapindaceae. This anomalous condition arises from the unusual position of the primary vascular bundles, which are not arranged in a circle but form a deeply-lobed ring; so that, by the development of interfascicular cambium, the cambium of each lobe is united into a separate cambium ring. Each of these rings, independently of the others, then gives rise to wood and bast (Fig. 204).

2. Epiphytes (103).—In another group of cormophytes the leaves obtain stronger light by the plants being able to establish themselves on the stems and branches of high trees instead of being rooted in the ground. Such plants are termed epiphytes. Since the trees only fford them support they may be replaced by inorganic substrata such as rocks. Only such plants as have seeds which will be carried by wind or animals to the branches of trees can adopt an epiphytic mode of life. The supply of the requisite water and nutrient salts will evidently be a difficulty. Consequently special adaptations are found to meet this; in many epiphytes shoot-tubers serve for water storage (*e.g.* in the Orchidaceae), being replenished in moist periods, or there may be adaptations to catch water more directly.

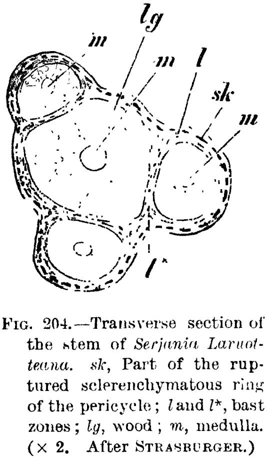


FIG. 204.—Transverse section of the stem of *Serjania Laruotteana*. *sk*, Part of the ruptured sclerenchymatous ring of the pericycle; *l* and *l**, bast zones; *lg*, wood; *m*, medulla. (× 2. After STRASBURGER.)

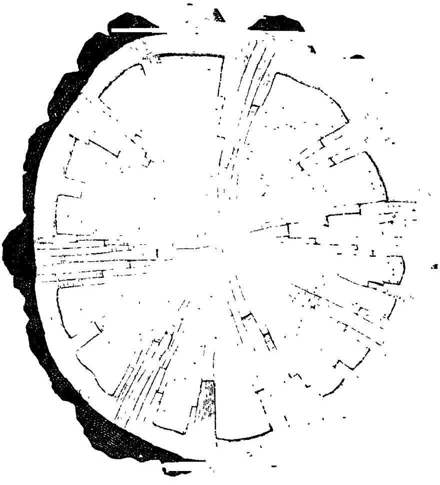


FIG. 205.—Transverse section of the stem of one of the Bignoniaceae. (Nat. size. After SCHENCK.)

In our latitudes epiphytes are represented only by some Algae, Lichens, and Bryophyta growing on the bark of trees; most of these can withstand dessication. In the tropics, however, many cormophytes live as epiphytes. These plants belong especially to the Pteridophyta and the families Orchidaceae, Bromeliaceae, and Araceae, etc.

Their difficulty in obtaining water explains why the tropical epiphytes are nearly all well-marked xerophytes (Fig. 191). They are fastened by ATTACHING ROOTS which are relatively short, unbranched, and negatively heliotropic, and grow round and clasp the branch on which the plant grows. In addition to these attaching roots, much longer ABSORBENT ROOTS are found in many Araceae, hanging down freely in the air without branching until they reach the soil.

Most epiphytes, however, have no connection with the ground and are dependent on the rainfall for their water-supply; they frequently have special arrangements for collecting and retaining this. The many-layered epidermis of the aerial roots of many Orchids, and of various Aroids, undergoes a peculiar modification and forms the so-called VELAMEN, a parchment-like sheath surrounding the roots, and often attaining a considerable thickness. The cells of this enveloping sheath are generally provided with spiral or reticulate thickenings, and lose their living contents. They then become filled with either water or air, depending upon the amount of moisture contained in the surrounding atmosphere. These root-envelopes absorb water like blotting-paper; when the velamen is filled with water the underlying tissues impart a greenish tint to the root; but if it contains only air the root appears white. In other epiphytic Orchidaceae and Araceae there are upwardly-directed roots forming a branched network in which falling leaves, etc., are caught and transformed into humus that retains moisture. Among the Ferns also there are epiphytes which collect humus by means of their leaves. In *Asplenium nidus* the leaves form a rosette enclosing a funnel-shaped cavity above the summit of the stem, and humus accumulates in this. In species of *Polypodium* and *Platycerium* special pocket-leaves and mantle-leaves serve for the accumulation of humus and water. The transformation of the leaves of the Asclepiadaceous plant *Dischidia rafflesiana* (Fig. 206) goes still further. Some of the leaves form deep pitchers with narrow mouths in which the water of transpiration becomes condensed; roots, which branch freely, grow into the pitchers, and obtain not only water but valuable nitrogenous substances. The pitchers are, in fact, usually tenanted by colonies of ants, and their excreta and remains form a source of food to the plant.

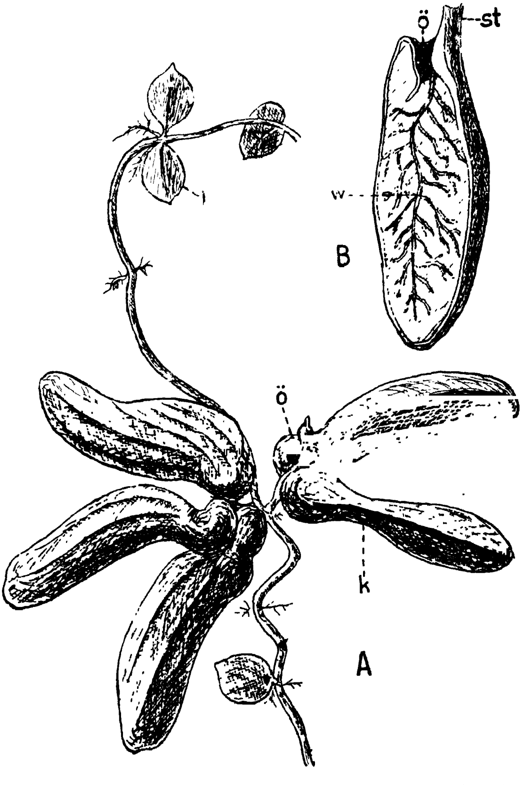


Fig. 206.—*A*, *Dischidia Rafflesiana* with foliage-leaves (*l*) and pitcher leaves (*k*). *B*, Pitcher cut longitudinally; *o*, opening; *st*, stalk; *w*, root. (*A* about ⅓, *B* about ½ nat. size. After Treub.)

The American Bromeliaceae afford an extreme type of epiphytic plants in which the roots may be completely wanting (*e.g. Tillandsia usneoides*) or serve for attachment only. The absorption of water is entirely by means of peculiar, expanded, peltate hairs borne on the leaves. In many of these plants water collects in the cavities formed by the closely associated leaf-bases, and the plants are spoken of as CISTERN EPIPHYTES.

(c) Adaptations of Green Cormophytes to special Modes of Nutrition

The so-called INSECTIVOROUS or CARNIVOROUS PLANTS must be referred to here (104). These are plants provided with arrangements for the capture and retention of small animals, especially insects, and for the subsequent solution, digestion, and absorption of the captured animals. All these insectivorous plants are provided with chlorophyll, and can thus live autotrophically.

A great variety of contrivances for the capture of insects are made use of by carnivorous plants. The leaves of *Drosera* are covered with peculiar emergences ("tentacles"), the stalks of which are traversed by vascular strands while the glandular extremities discharge a viscid acid secretion (Figs. 207, 208). A small insect which comes in contact with any of the tentacles is caught in the sticky secretion, and in its ineffectual struggle to free itself only comes in contact with other glands and is even more securely held. Excited by the contact-stimulus, all the other tentacles curve over and close upon the captured insect, while the leaf-blade itself becomes concave and surrounds the small prisoner more closely.

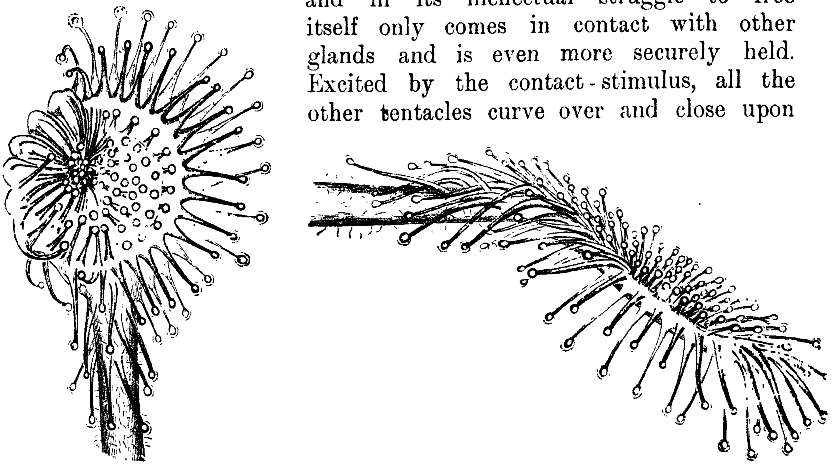


FIG. 207.—Leaves of *Drosera rotundifolia*. That on the left with its partly incurved tentacles is viewed from above, that on the right with expanded tentacles from the side. (× 4. After DARWIN.)

In *Pinguicula* it is the leaf margins which fold over any small insects that may be held by the minute epidermal glands. In species of *Utricularia* (Fig. 209), which grow frequently in stagnant water, small green bladders (metamorphosed leaf-segments) are found on the dissected leaves. In each bladder, which is filled with water, there is a small quadrangular opening closed by an elastic valve, which only opens inwards. If small aquatic animals, especially crustaceans come in contact with one of the four lever-like bristles projecting from the lower margin of the lid of the bladder or with the lid itself, they are drawn into the bladder by a peculiar "gulping movement"; this comes about by the release of the elastic tension of the wall, dependent on a cohesion mechanism (cf. p. 336). The valve springs back into place and closes the opening so that the animals are imprisoned. Hairs projecting from the inner surface of the bladder absorb the digested remains of the animals and also some of the water. In this way the condition of elastic tension is re-establised and the bladder is again ready to perform the gulping movement ([105]).

More remarkable still, and even better adapted for its purpose, is the mechanism exhibited by some exotic insectivorous plants. In the case of Venus's fly-trap (*Dionaea*), growing in the peat-bogs of North Carolina, the capture of insects is effected by the sudden closing together of the two halves of the leaf, which are fringed with long bristles. Fig. 210 shows a leaf of *Dionaea* in the expanded condition, ready for the capture of an insect.

The rare European water-plant *Aldrovanda* has similarly formed leaves.

In the case of other exotic insectivorous plants (*Nepenthes*, *Cephalotus*, *Sarracenia*, *Darlingtonia*), the traps for the capture of animal-food are formed by the leaves which grow in the shape of pitchers (Figs. 211, 212). The leaves of *Nepenthes*, for example, have the form of pitchers which are usually roofed over by a lid that probably serves to keep the rain-water out; the pitcher, as GOEBEL has shown, arises as a modification of the leaf-blade. At the same time the leaf-base becomes expanded into a leaf-like body, while the petiole between the two parts sometimes fulfils the office of a tendril. These trap-like receptacles are partially filled with a watery fluid excreted from glands on their inner surfaces. Enticed by secretions of honey

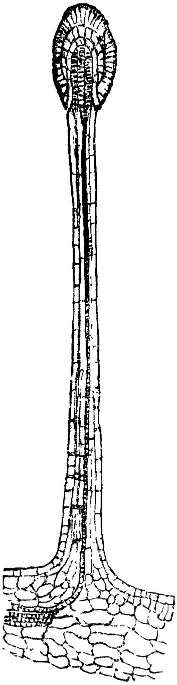


FIG. 208.—Tentacle of *Drosera rotundifolia*. (× 60. After STRASBURGER.)

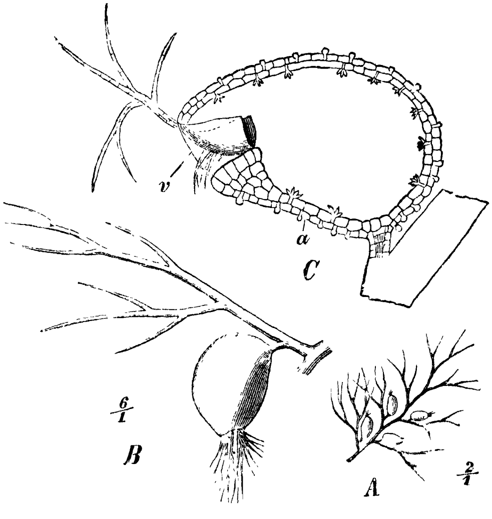


FIG. 209.—*Utricularia vulgaris*. *A*, Part of leaf with several bladders (× 2). *B*, Single pinnule of leaf with bladder (× 6). *C*, Longitudinal section of a bladder (× 28); *v*, valve; *a*, wall of bladder. (*A*, *B*, after SCHENCK; *C*, after GOEBEL.)

to the rim of the pitcher (in the case of *Nepenthes*), and then slipping on the smooth surface below the margin, insects and other small animals fall into the fluid. They are prevented from climbing out by the smooth waxy covering of the inside of the pitcher.

B. Heterotrophic Cormophytes (106)

The green cormophytes utilise the light and by means of their chlorophyll construct organic substance from carbon-dioxide and water; they also require to transpire in order to accumulate the nutrient salts from the soil in sufficient amount. Besides these forms others, which obtain some or all of their organic substance directly from the environment, are met with among cormophytes, just as they occur among the thalloid plants. They do not depend upon light or transpiration, and frequently live at the expense of other living organisms as PARASITES. The peculiar form of these plants and the contrast they present to the green cormophytes are related to their special mode of nutrition. From the changes in their external appearance it is evident how far-reaching is the influence exercised by the chlorophyll. With the diminution or complete disappearance of chlorophyll, the development of large leaf-surfaces, so especially fitted for the work of assimilation and transpiration, is discontinued. The leaves shrink to insignificant scales, or are completely wanting. The stems also are greatly reduced and, like the leaves, have a yellow instead of a green colour. Since there is no active transpiration the roots in many forms are reduced. Consequently the xylem portion of the vascular bundle remains weak, and secondary wood is feebly developed. In contrast to these processes of reduction resulting from a cessation of assimilation, there is the newly-developed power in the case of parasites to penetrate other living organisms (the hosts) and to deprive them of their assimilated products.

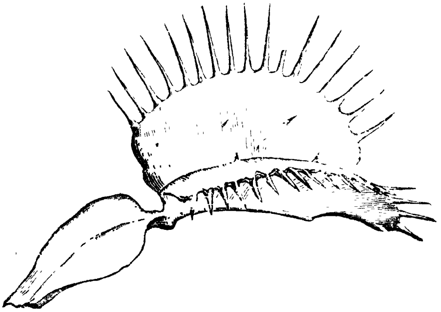


FIG. 210.—A leaf of *Dionaea muscipula*, showing the sensitive bristles on its upper surface, which, in the parts shaded, is also thickly beset with digestive glands. (× 4. After DARWIN.)

Some exotic parasitic plants, especially the Rafflesiaceae, have become so completely transformed by their parasitic mode of life that they develop no apparent vegetative body at all, and do not show the characteristic segmentation of cormophytic plants, but grow altogether within their host-plant, whence they send out at intervals their extraordinary flowers. In the case of *Pilostyles*, a parasite which lives on some shrubby Leguminosae, the whole vegetative body is broken up into filaments of cells which penetrate the host-plant like the mycelium of a fungus. The flowers alone become visible and protrude from the stems and leaf-stalks of the host-plant (Fig. 213). The largest known flower, which attains a diameter of 1 metre, is that of the Sumatran parasitic plant *Rafflesia Arnoldi*; it is seated immediately on the roots of its host-plant, which is a species of *Cissus*.

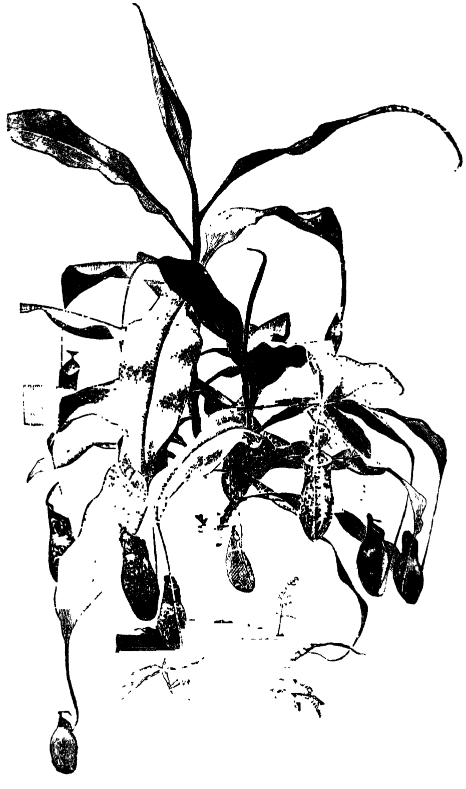


FIG. 211.—*Nepenthes robusta*. (⅓ nat. size. After SCHENCK.)

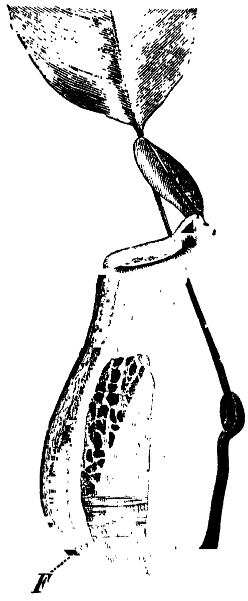


FIG. 212.—Pitchered leaf of a *Nepenthes*. A portion of the lateral wall of the pitcher has been removed in order to show the digestive fluid (*F*), excreted by the leaf-glands. (½ nat. size. After NOLL.)

Cuscuta europea (Fig. 214), a plant belonging to the family of the Convolvulaceae, may be cited as an example of a parasitic Phanerogam. Although, owing to the possession of chlorophyll, it seems to some extent to resemble normally assimilating plants, the amount of chlorophyll present is in reality so small that it is evident that *Cuscuta* (Dodder) affords an example of a very complete parasite. The embryonic *Cuscuta* plantlet, coiled up in the seeds, pushes up from the ground in the spring, but even then it makes no use of its cotyledons as a means of nourishment; they always remain in an undeveloped condition (Fig. 214 at the right). Nor does any underground root-system develop from the young rootlet, which soon dies off The seedling becomes at once drawn out into a long thin filament, the free end of which moves in wide circles, and so inevitably discovers any plant, available as a host, that may be growing within its reach. In case its search for a host-plant is unsuccessful, the seedling is still able to creep a short distance farther at the expense of the nourishing matter drawn from the other extremity of the filament, which then dies off (*t*) as the growing extremity lengthens. If the free end, in the course of its circling movements, comes ultimately into contact with a suitable host-plant, such as, for example, the stem of a Nettle or a young Willow shoot (Fig. 214 in the centre), it twines closely about it like a climbing plant. Papillose protuberances of the epidermis are developed on the side of the parasitic stem in contact with the host-plant, and pierce the tissue of the host. If the conditions are favourable, these PRE-HAUSTORIA are soon followed by special organs of absorption, the HAUSTORIA (*H*). These arise from the internal tissues of the parasite, and possess, in a marked

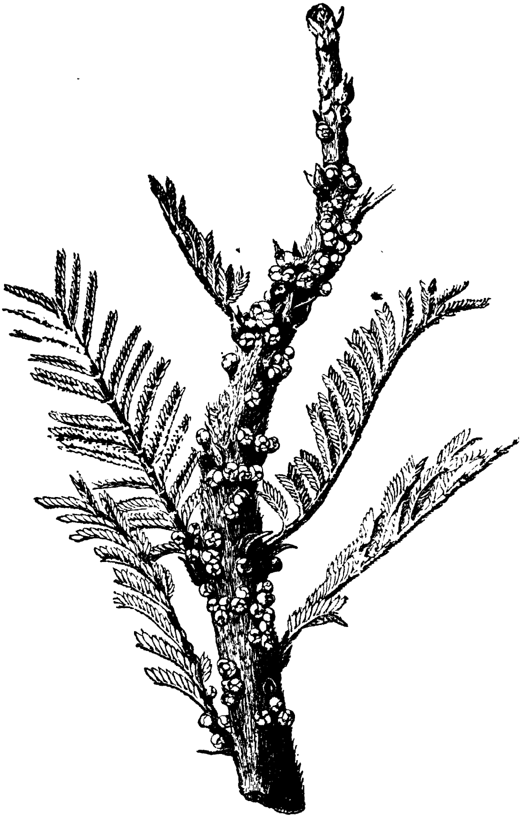


FIG. 213.- Branch of a leguminous plant from the surface of which the flowers of a parasitic plant (*Pilostyles Ulei*, Solms, belonging to the Rafflesiaceae) are protruding. (From GOEBEL'S *Organography*.)

degree, the capability of penetrating to a considerable depth into the body of the host-plant. They invade the tissues of the host, apparently without difficulty, and fasten themselves closely upon its vascular bundles, while single hypha-like filaments produced from the main part of the haustoria penetrate the soft parenchyma and absorb nourishment from the cells. A direct connection is formed between the xylem and phloem of the bundles of the host-plant and the conducting system of the parasite, for in the thin-walled tissue of the haustoria there now develop both wood and sieve-tube elements, which connect the corresponding elements of the host with those of the parasitic stem (Fig. 214 at the left). Like an actual lateral organ of the host-plant, the parasite draws its transpiration water from the xylem, and its plastic nutrient matter from the phloem of its host.

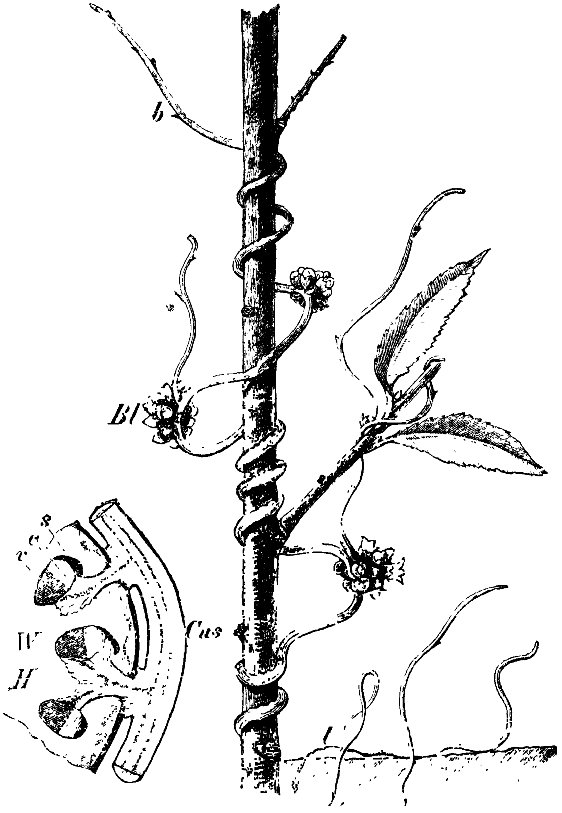


FIG. 214.—*Cuscuta europaea.* On the right, germinating seedlings. In the middle, a plant of *Cuscuta* parasitic on a Willow twig; *b*, reduced leaves; *Bl*, flower-clusters. On the left, cross-section of the host-plant *W*; showing haustoria *H* of the parasite *Cus*, penetrating the cortical parenchyma and in intimate contact with the xylem *v* and the phloem *c* of the vascular bundles; *s*, displaced cap of sheathing sclerenchyma. (After NOLL.)

The seeds of *Orobanche* (Broom Rape), another parasite, only germinate when in contact with the roots of the host-plant; only its haustoria penetrate the roots, and its light yellow, reddish-brown, or amethyst-coloured flower-shoot appears above the surface of the ground. *Orobanche* (Fig. 792), like *Cuscuta*, contains a small amount of chlorophyll. Both are dreaded pests; they inflict serious damage upon cultivated plants, and are difficult to exterminate.

A similar appearance to *Orobanche* is presented by some plants which grow in the humus soil of woods: certain Orchids (*Neottia*, *Coralliorrhiza*, *Epipogon*) and *Monotropa*. The absence of chlorophyll, the reduction of the leaves to scales, and (in *Coralliorrhiza*) the absence of roots also (cf. Fig. 215), are indications that these plants obtain organic material from without.

In contrast to parasites, which have come to be wholly dependent on their host-plants, there are others which have well-developed green leaves and are capable of assimilation. Good examples are afforded by our native Mistletoe (Fig. 652) and other exotic Loranthaceae (cf. p. 262) which are parasitic on trees.

II. Organs of Reproduction (107)

A. Significance of Reproduction to the Organism.—A natural or an accidental death is the end of every organism. For the maintenance of living beings reproduction is thus as essential as nutrition. The main feature of reproduction consists in portions of an individual continuing after its death, and possessing the power of developing into new individuals. The simplest type of reproduction is met with in the division into two and the separation of the daughter-cells of many unicellular plants. Some simply organised, multicellular Thallophytes, such as *Spirogyra*, are not far removed from this; the filament falls into the constituent single cells, and each of these, by repeated cell-division, gives rise to a new multicellular individual. As a rule, however, reproduction involves the formation of special germs which are separated from the parent-plant, and later, on germination, give rise to young daughter-organisms which grow into new individuals like the parent.

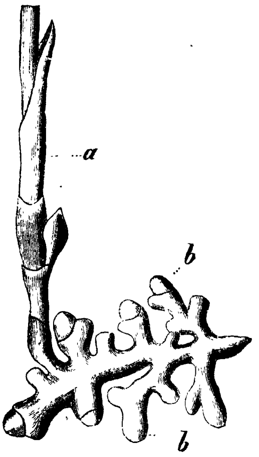


FIG. 215.—Rhizome of *Corallorrhiza innata*. *a*, Floral shoot; *b*, rudiments of new rhizome branches. (Nat. size. After SCHACHT.)

While in the unicellular and in simpler multicellular plants every cell can serve for reproduction, in all the more highly organised plants a division of labour is apparent between vegetative organs and reproductive organs. The latter are specially constructed for the production of reproductive cells or germs. With the higher organisation of the plants, the division of labour becomes increasingly marked and parts of the body are now definitely devoted to reproduction. The subdivision of the vegetable kingdom into Classes, Orders, Families, etc., is based in the first place on the diversity of structure and position of the organs of reproduction.

B. General Properties of the Germs.—The construction of the germs, as in the case of the vegetative organs, is closely connected with the purposes they have to serve.

The small size of most reproductive bodies, in comparison with the parent-organism, is characteristic. The parent-plant can thus produce numerous germs without excessive expenditure of material, while at the same time the distribution of the germs is facilitated.

The object of reproduction is not merely the production of a new individual in place of the parent, but an increase in the number of individuals. Since the majority of the germs may not meet with favourable conditions for their germination and growth, and a large number will perish before they can in turn reproduce, the production of only a single germ would result in the speedy extinction of the species. An apparently prodigal production of germs is thus the rule. A cap-fungus or a fern may form millions of spores; a poplar tree, according to BESSEY, may ripen twenty-eight million seeds annually.

Provision is further necessary for the separation of the germs from the parent and their dispersal widely from it. In the immediate neighbourhood there may not be the conditions for germination, or there may be no room for the development of the progeny.

Lastly, it is necessary for the germs to be provided with reserve food-materials from the parent-organism, in order that their development, until they are able to nourish themselves, should be ensured.

Frequently the reproductive bodies serve to carry the organism over cold or dry periods that are unfavourable to active life. They pass into a resting condition (p. 205), in which they are more resistant to injurious influences (desiccation, frost, heat, poisons). Such germs are usually thick-walled, and only germinate on the return of favourable conditions.

C. Types of Reproductive Bodies.—The germs which can develop into plant-bodies composed of many cells may themselves be unicellular (spores) or multicellular (gemmae and seeds). Two types of reproduction are readily distinguished in plants of nearly all the classes of the vegetable kingdom.

In the first type, cells or multicellular bodies are formed which can develop into a new independent individual on their separation from the parent, either at once or after a period of rest. This kind of reproduction is termed VEGETATIVE, ASEXUAL, or MONOGENETIC.

In SEXUAL REPRODUCTION, the second of the two modes of reproduction, two kinds of reproductive cells, each of which carries the characters of the organism producing it, are formed, but neither is directly capable of further development, and both perish in a very short time, unless opportunity is given for their fusion with each other. Not until the one cell has fused with the other cell (FERTILISATION) does the product acquire the capacity of development and growth. This mode of reproduction is termed SEXUAL or DIGENETIC reproduction.

Most plants have both methods of reproduction. Sexual reproduction is wanting only in the lowest groups (the Bacteria, Cyanophyceae, and some Algae and Fungi).

In certain exceptional cases a sexual cell may proceed to develop further without fertilisation. This is termed PARTHENOGENESIS (108). This has been found in the vegetable kingdom in *Chara crinita*, one of the Algae, and in the development of the embryo from the unfertilised ovum in a number of families of higher plants (Compositae, Ranunculaceae, Rosiflorae, Thymeleaceae, Urticaceae), and in the Marsiliaceae.

In all these plants the parthenogenesis is regular and habitual, the egg-cell developing without further stimulus. In other cases, which may be termed experimental parthenogenesis, the development follows experimental interference.

The process of fertilisation of sexual cells may, in particular cases, be replaced by the fusion of the nuclei of adjoining vegetative cells (109). This is the case in the prothallium of certain cultivated forms of Ferns (*e.g.* of *Dryopteris* (*Lastraea*) and *Athyrium*). The product of this fusion effects the reproduction, the sexual organs of the prothallium being reduced.

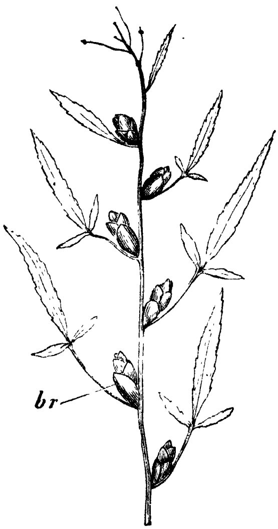


FIG. 216.—Shoot of *Dentaria bulbifera*, bearing bulbils, *br*. (Nat. size. After SCHENCK.)

A full comprehension of the phenomena of reproduction requires the study of the developmental history in the various groups of plants. This is treated of in the Special Part of this work. Only the facts and problems concerning the processes of reproduction, which are important for general morphology, will be dealt with here.

1. Multiplication by Multicellular Vegetative Bodies (Budding)

This occurs in many Bryophyta, *e.g.* in *Marchantia*, where the gemmae are formed in special receptacles on the thallus (Figs. 463, 464). It is also widely spread in the form of budding in Pteridophyta and Phanerogams.

Specially-formed lateral shoots serving to reproduce the plant are seen in the runners or stolons produced above or below ground by many plants. The RUNNERS of the Strawberry are slender cylindrical branches from the axils of the leaves of the rosette; they root from the terminal bud, which becomes independent by the subsequent decay of the runner. Many BULBS and TUBERS serve for reproduction in the higher plants, as do also BULBILS (Fig. 216) and the winter-buds which become detached as the HIBERNACULA of a number of aquatic plants (*e.g. Hydrocharis, Stratiotes*).

Buds may also arise in places where no growing points are normally present; they are then adventitious (cf. p. 118).

Many herbaceous perennials, without forming special organs of vegetative reproduction, increase in number of individuals by the decay of the older portions of their branched rhizomes isolating the branches. Among Sea-weeds also the mechanical action of the surf may separate portions of the thallus which can grow into new thalli. *Caulerpa* is propagated in this fashion.

2. The Formation of Reproductive Cells

(a) Asexual Reproductive Cells (Spores).—These originate in two ways. 1. In many Fungi germ-cells are isolated by budding and constriction from certain hyphae as EXOSPORES or CONIDIOSPORES (Fig. 217*c*). 2. In other Fungi, in the majority of the Algae, in Bryophyta, and in Pteridophyta, the asexual cells originate as ENDOSPORES or SPORANGIAL SPORES in special receptacles (SPORANGIA), and emerge through openings in the wall of these (Figs. 218 s^2, 222 *sp*). These sporangia in the Thallophyta are single cells, the protoplast of which usually divides to give rise to several or many endospores (Fig. 222 *sp*). In the Bryophyta and Pteridophyta the asexual cells are always developed in special sporangia of more complicated structure than in the Thallophyta. These sporangia are multicellular structures,

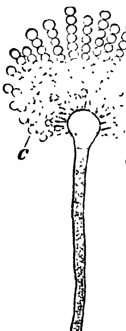


FIG. 217.—Conidiophore of *Aspergillus herbariorum*. (× 540. After KNY.)

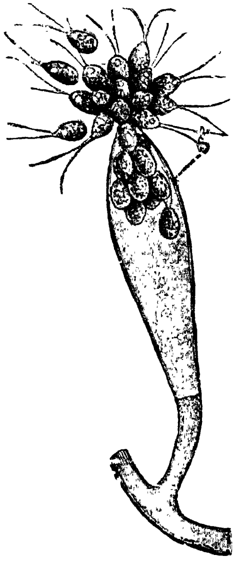


FIG. 218.—*Saprolegnia mixta*. Sporangium from which the biciliate zoospores (s^2) are escaping. (After G. KLEBS.)

one or more outer layers of cells forming the wall, and the enclosed cells constituting the sporogenous tissue (Fig. 219 *sg*).

The asexual spores of the Thallophyta are in part adapted to distribution by means of water, as in the case of many sporangial spores of Algae and Fungi. These spores are naked, without a cell-wall, and as a rule are able to move through the water by the aid of cilia (Figs. 218, 220 *A*). They are termed SWARM-SPORES or ZOOSPORES.

The spores of other Thallophyta and of the Bryophyta and Pteridophyta are adapted to dispersal by wind. They are very small and light, surrounded by thick walls and resistant to drying.

(b) Sexual Reproductive Cells. Gametes. 1. Different Forms of Sexual Cells and Sexual Organs.—A great variety in the methods of sexual reproduction is shown by plants; different as the extremes are, however, they are connected by intermediate links.

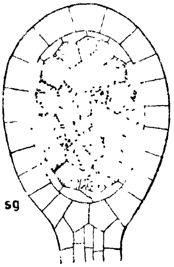


FIG. 219. — Diagram of the sporangium of a Pteridophyte, the sporogenous tissue (*sg*) being enclosed by a sterile wall.

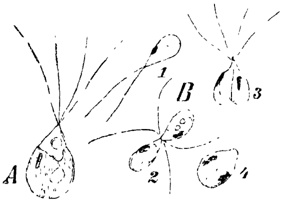


FIG. 220.– *Ulothrix zonata*. *A*, Asexual swarm-spore; *B1*, a gamete; *B2*, *B3*, conjugating gametes; *B4*, zygote resulting from conjugation. (× 500. After STRASBURGER.)

In the simplest types of sexual reproduction met with in the lower Algae and Fungi, the sexual cells or GAMETES are usually naked protoplasts of similar size and structure; these resemble the asexual swarm-spores but conjugate with one another (ISOGAMY, Fig. 220 *B*). They develop, singly or in numbers, from the protoplasts of certain cells termed GAMETANGIA, the process resembling the origin of the swarm-spores. The product resulting from the conjugation of the gametes is called a ZYGOTE or ZYGOSPORE (Fig. 220 *B* 4). The facts are in favour of regarding the gametes as homologous with the swarm-spores, from which they often differ only in their smaller size, and the gametangia as homologous with sporangia. By this is meant that the gametes and gametangia have been derived phylogenetically by the modification of swarm-spores and sporangia. Such gametes are capable of active movement by means of cilia; they seek one another in the water and unite in pairs (Fig. 220 *B*).

The gametes, however, frequently differ in size in the Algae and

Fungi, and this is the rule in the Bryophyta and Pteridophyta. The larger gametes, which contain abundant reserve-materials, are female (♀) and the smaller are male (♂). The female gamete may be non-motile when it is known as an egg-cell (OOSPHERE). In this case the small SPERMATOZOID seeks out and fertilises the large EGG-CELL (OOGAMY). In the case of oogamy the gametangia are usually unlike. In the Thallophyta, the cells in which the small naked spermatozoids arise in large numbers are termed ANTHERIDIA (Figs. 221, 2 *a*; 222 *a*), while those within which one or more egg-cells are formed are the OOGONIA (Figs. 221, 2; 222 $o_{,}$, $o_{,,}$). In the Bryophyta and Pteridophyta on the other hand the small antheridia (Fig. 223, 1) have a wall of sterile cells enclosing the spermatogenous tissue from which the spermatozoids are developed; similarly the egg-cell is enclosed in a small, multicellular organ called an archegonium (Fig. 223, 2).

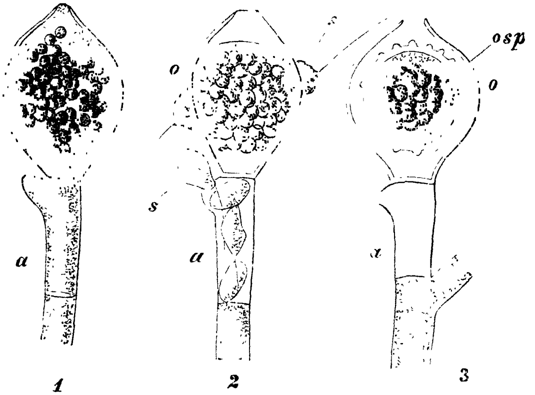


FIG. 221.—*Monoblepharis sphaerica.* End of filament with terminal oogonium (*o*) and an antheridium (*a*). 1. Before the formation of the egg-cells and spermatozoids. 2. Spermatozoids (*s*) escaping and approaching the opening of the oogonium. 3. *osp*, ripe oospore, and an empty antheridium. (× 800. After CORNU.)

Numerous transitions in the Thallophyta between the two conditions show clearly that oogamy has been derived phylogenetically from isogamy by way of heterogamy. From this it follows that the antheridia and oogonia of Thallophyta are homologous with one another, and also with the gametangia of the isogamous Algae and Fungi (cf. also Fig. 222).

The egg-cell (oosphere) which is usually naked, frequently remains in the female sexual organ, in the wall of which an opening forms (Fig. 221, 2; 222 $o_{,}$, $o_{,,}$, ö; 223, 2). Fertilisation of the receptive oosphere results from the ciliated spermatozoids which have been liberated into the surrounding water, being chemotactically attracted (cf. p. 331) by substances excreted from the egg-cell. A single spermatozoid then fuses with the egg-cell.

The fertilised oosphere surrounds itself with a cell-wall and is now able either immediately, or after a period of rest as an OOSPORE (Fig. 221; 3 *osp*), to develop further. In the Bryophyta and Pteridophyta there arises by cell-division from the fertilised egg a mass of meristematic cells constituting the EMBRYO, which grows on into the young plant.

The sexual organs of the Spermatophyta have come to differ from those of the simpler types in ways that are not easy to characterise briefly. The male sexual cells are enclosed in the pollen-grains, and the female sexual cell or cells in the ovules of the flower. From this it follows that the fertilisation of the egg-cell in Spermatophyta takes place in a special way by the growth of a pollen-tube, after pollination (cf. the special part).

2. The Process of Cell-Fusion in Fertilisation and its Results.—The actual process of fertilisation in its simplest form can be best observed in those lower organisms with similar gametes (Fig. 220). In these it can be easily shown that not only the cytoplasm of the two cells but sooner or later the nuclei also fuse. This fusion is the essence of fertilisation; also, in all cases of heterogamy and oogamy, the sexual nuclei come together in the zygote and ultimately fuse. When the male-cell possesses chromatophores, which in many Algae (Florideae, *Chara*, etc.) is not the case, they do not fuse with those of the female-cell. They either coexist in the fertilised cell or, when a constant number of chromatophores is maintained, disappear.

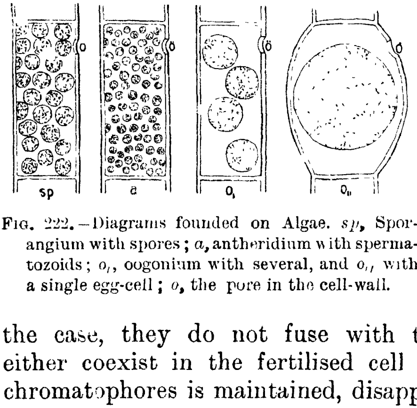


FIG. 222.—Diagrams founded on Algae. *sp*, Sporangium with spores; *a*, antheridium with spermatozoids; $o_{,}$, oogonium with several, and $o_{,,}$, with a single egg-cell; *o*, the pore in the cell-wall.

In the typical process of nuclear division it has been seen that the nuclei of an individual possess a constant number of chromosomes characteristic of the species. The male gamete thus contributes as many chromosomes as the female gamete. These chromosomes do not fuse in the conjugation of the sexual nuclei, so that the nucleus of the zygote has double the number of chromosomes possessed by the sexual cells. It is DIPLOID and contrasts with the HAPLOID nuclei of the gametes.

The nuclei resulting from the further division of the nucleus of the zygote are as a rule diploid; in each there are as many chromosomes derived from the male- as from the female-nucleus. When the chromosomes of the haploid cells are characterised by differences in size and shape which are apparent at each nuclear division, the diploid nuclei show pairs of chromosomes of each size. These similar chromosomes, the one derived from the male- and the other from the female-parent, as a rule, lie in pairs in the nuclear plate Fig. 14).

Since the nuclei of the sexual cells of all the individuals of a race are always haploid, while the conjugation nucleus and as a rule the products of its division are diploid, there must be a change from the diploid to the haploid condition at some point in the developmental history of the individual. Were this not so, the number of chromosomes would double with each generation. The change is effected at the REDUCTION DIVISION (12), which is a peculiar nuclear division in which there is a separation to form the daughter-nuclei of entire chromosomes, and not half-chromosomes resulting from longitudinal splitting. This occurs at a definite point in the development, which, however, differs in different organisms. Thus a regular alternation of the haploid and diploid phases of the nucleus is characteristic of the ontogenetic development of sexual organisms.

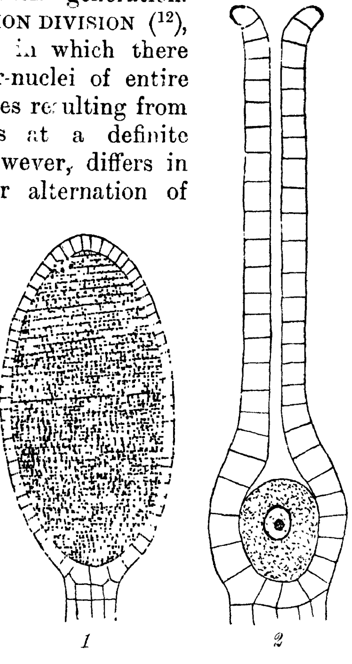


Fig. 223.—1. Antheridium, with wall of sterile cells enclosing the spermatogenous tissue. 2. Archegonium, with corresponding wall and an egg-cell. Both based on a Liverwort.

The reduction-division in contrast to the typical division is termed HETEROTYPIC, and is also spoken of as MEIOSIS. It is characteristic of this, that in the spireme stage of the prophase the nuclear contents become for a period contracted together at one side (SYNAPSIS, Fig. 224, 2, 3). It is further characteristic of the succeeding stages that the paternal and maternal chromosomes become associated in pairs or GEMINI (PARASYNDESIS) or more completely united. The number of these GEMINI is half as great as the number of chromosomes in the tissue-cells of the same plant, since two chromosomes are represented by each geminus. The paired chromosomes become shorter and thicker and are distributed around the periphery of the nucleus; this is the condition that has been termed DIAKINESIS (5, 6). At this stage kinoplasmic filaments are becoming applied to the nuclear membrane (6); the latter disappears, and the nuclear spindle, which is at first multipolar (7) but ultimately becomes bipolar (8), originates from the kinoplasmic fibres. The paired chromosomes become attached to the fibres of the spindle and arranged in an equatorial nuclear plate (8). Shortly afterwards the separation of the chromosomes, until now united in pairs, takes place (9). IN THIS PROCESS, IN WHICH THE ESSENTIAL OF THE REDUCTION-DIVISION IS EFFECTED, IT IS NOT LONGITUDINAL HALVES OF CHROMOSOMES BUT ENTIRE CHROMOSOMES WHICH SEPARATE FROM ONE ANOTHER. The result of this is that each daughter-nucleus receives only half as many chromosomes as were found in the tissue-cells of the same plant, and that these chromosomes may be male or female. Since chromosomes of corresponding lengths are always associated in the gemini, one being derived from the male and the other from the female parent, and these chromosomes separate from one another in the reduction-division, each haploid daughter-nucleus must inherit some chromosomes from the father, and others from the mother. Which chromosomes come from the one or other parent appears to be determined by chance. The formation of the daughter-nuclei is completed (10) as in an ordinary division, but following promptly on the first reduction-division, which is also known as the HETEROTYPE division, comes a second or HOMOTYPE division, which in all essentials follows the typical course (11, 12). Thus two rapidly-succeeding nuclear divisions (TETRAD-FORMATION) are characteristic of most cases of reduction. In the homotypic division longitudinal halves of chromosomes separate as in the typical division. A difference from the latter is that the chromosomes are not split longitudinally in the prophase of the homotypic division itself, but, as it seems, were already split in the prophase of the preceding reduction-division without the halves thus formed separating.

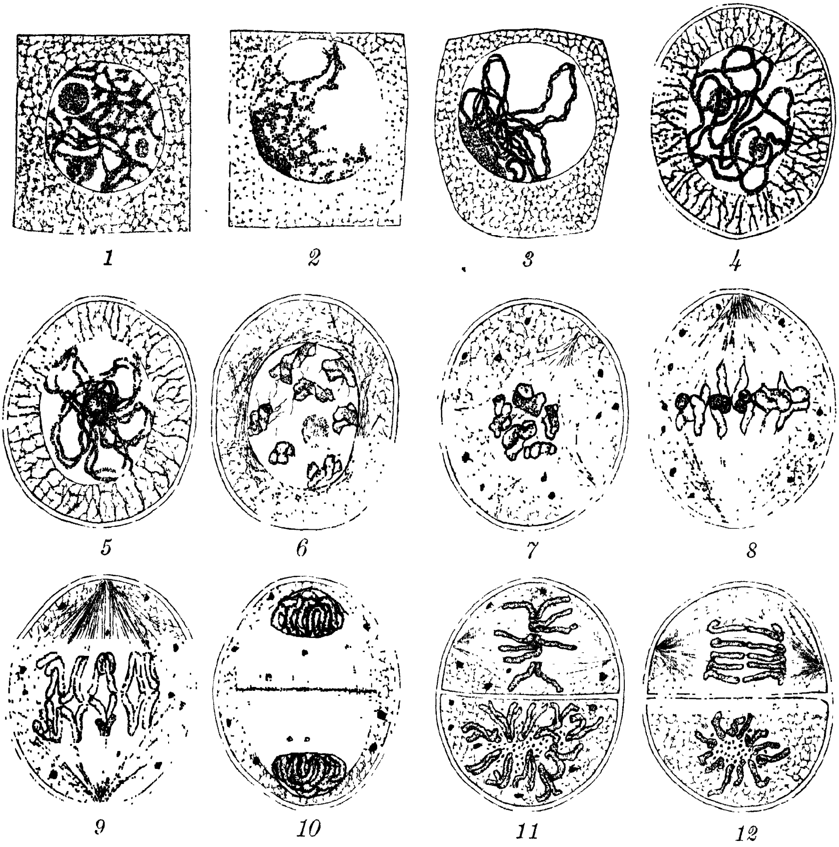


FIG. 224.—Pollen-mother-cell of a Lily in division, somewhat diagrammatic. Further description in text. (After STRASBURGER.)

It appears possible that an exchange of substance takes place between the chromosomes when they are associated in pairs (110).

The fundamental difference between the somatic nuclear division and the reduction-division may be made clearer by means of a diagram. Fig. 225 *A* represents a somatic division with longitudinal splitting of the chromosomes. In *A a* six longitudinally split chromosomes, distinguished by the different shading, are shown arranged to form the nuclear plate. The two middle ones are seen from the end, the others from the side. In *A b* the separated halves of these chromosomes are shown on their way to the poles of the spindle in order to form the daughter-nuclei. In Fig. 225 *B* the reduction-division is diagrammatically represented. The six chromosomes of Fig. 225 *A* are shown in *B a* similarly shaded and united in three gemini. The two lateral gemini are seen from the side, the middle one from the end. In *B b* the chromosomes of each geminus have separated and are moving towards the poles of the spindle to form the two daughter-nuclei. This division results in a reduction of the chromosome-number from six to three. In contrast to this reduction-division, which, because whole chromosomes separate, results in a definite difference of the products of division, may be placed the somatic nuclear division. This, since the longitudinal halving of the chromosomes gives rise to completely equivalent products of division, may be termed equation division.

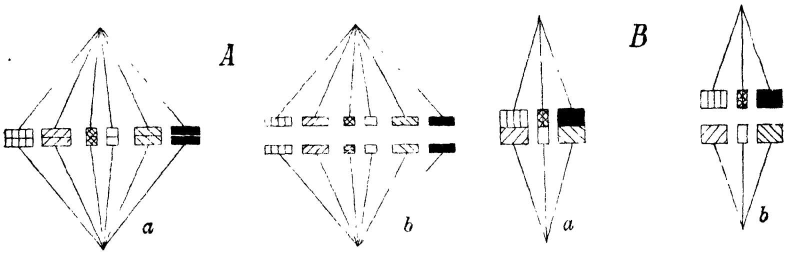


FIG. 225.—Diagrammatic representation of ordinary nuclear division (*A*) and of the reduction-division (*B*). (After STRASBURGER.)

D. Alternation of Generations (111).—In plants there is frequently an alternation of at least two generations differing in their modes of reproduction; these may be morphologically distinct and independent individuals. The life-history of such a plant is thus composed of two kinds of individuals, which regularly alternate with one another, are frequently very different in form and structure, and bear different reproductive organs. The reproduction of the one generation (sporophyte) is asexual; that of the other (gametophyte) is sexual. The Fern may be taken as a typical example. The leafy fern-plant is the sporophyte, and produces only asexual spores. The spore on being shed does not grow into a new fern-plant, but into a small thalloid structure known as the prothallium (Fig. 93), which is the gametophyte, and reproduces sexually. The fertilised egg-cell develops into a leafy fern-plant. The reproductive cells of the one generation give rise to the other generation, and there is thus a regular alternation of the sporophyte and gametophyte and therefore of asexual and sexual reproduction.

Frequently the two generations are not represented by independent individuals, but the one remains permanently connected to the other like a parasite on its host plant. Careful investigation may then be required to establish the existence of an alternation of generations. This is the case for the Bryophyta and the Seed-plants.

When there is an alternation of generations the alternation of phases of the nucleus (cf. p. 189) tends to be connected with it. Thus, for example, the leafy sporophyte of the Fern is diploid (diplophase), and the fern-prothallus on the other hand haploid (haplophase). Nevertheless the alternation of nuclear phases is essentially distinct from the alternation of generations. Numerous lower organisms reproducing sexually, have an alternation of nuclear phases, although an alternation of generations is wanting.

There are certain remarkable cases in which the one generation develops from the vegetative cells of the other without change in the number of chromosomes. In a variety of *Athyrium filix foemina* the fern-plant arises without nuclear fusion from vegetative prothallial cells with diploid nuclei; without any production of spores, or the occurrence of a reduction-division, the diploid cells of the leaf-margin produce diploid prothallia (APOSPORY). According to YAMANOUCHI (in *Nephrodium molle*) a haploid prothallial cell may, without nuclear-fusion, give rise to a haploid fern-plant. Further, it is possible to obtain experimentally, on the regeneration of cut portions of the stalks of moss-capsules, a diploid moss-plant, *i.e.* a diploid gametophyte; this produces diploid sexual cells that are capable of fertilisation. Tetraploid moss-capsules are the result, and from these again by regeneration tetraploid moss-plants have been obtained. It is evident, therefore, that there is not a direct connection between the chromosome number and the construction of the two generations (107, 108).

SECTION IV

THE THEORY OF DESCENT AND THE ORIGIN OF ADAPTATIONS

A. The Theory of Descent (112).—How the organic forms living on the earth with their morphological peculiarities have arisen is one of the most important theoretical questions in morphology. The assumption once made that the kinds of plants were independently created (theory of special creation) has become gradually abandoned in favour of a theory of evolution, especially owing to the deepening of morphological knowledge and the influence of the work of DARWIN. This has already been referred to in the Introduction. The theory of evolution regards the existing organisms as developed from other and frequently more simply constructed forms which lived in earlier periods of the earth's history (cf. p. 1 ff.). This fundamental biological theory now permeates morphological investigation so completely that it is indispensable for the morphologist to be acquainted with the evidence for it. Evidence is afforded by classification, morphology, the geographical distribution of plants and animals, and by palaeontology.

1. EVIDENCE FROM CLASSIFICATION.—According to the theory of special creation the various species of plants were created independently and are essentially constant. They were supposed to be so little subject to change that one species could not arise from another; at most a species could give rise to more or less inheritable varieties. This view thus assumes that there are sharp limits between the species, and also that there is an essential difference between species and varieties. As the student of classification proceeds to examine any group of organic forms he finds that there are no characters to be relied on to distinguish varieties from species. The amount of morphological difference between the species of a genus, the varieties of a species, or between species and varieties, is quite undetermined. It has also come to be recognised that species are not independent morphological units but in many cases are comprehensive groups of forms or *petites espèces* (*e.g.* in the genera *Erophila*, *Rubus*, *Rosa*, *Hieracium*, *Quercus*). The sharp differentiation of such species from other species, *i.e.* other groups of forms, is frequently difficult or scarcely possible. The constant small species often differ less than do many so-called varieties. It thus becomes a matter of taste or "systematic sense" whether a particular form should be regarded as a species or a variety and how a species should be delimited. The rule formerly relied upon, that crosses between two independently created species would be sterile while those between two varieties of a species would be fertile, has proved untrustworthy; fertile and sterile hybrids are known both between two varieties and two species. There are not only transitions between species but between genera and even families, so that in these cases also the limits have to be drawn at the discretion of the systematist. All these facts only become comprehensible if it is assumed that species were not independently created but are capable of heredity with variation, so that new species can be derived from others by inherited changes, while more marked changes give rise to new genera or families. On any other assumption it remains inconceivable why organisms can be placed in groups of lower and higher order (species, genera, families, classes, etc.), which are in part coordinate (like the species of a genus or the genera of a family) and in part subordinated to others (like the species to the genus or the genera to the family); further, that the groups of extinct organisms which lived in earlier geological periods can as a rule be naturally placed in the same classification as the existing forms. All these difficulties disappear when organisms are regarded as blood-relations,

and the natural system as expressing their nearer or more distant relationship, and thus in a certain degree, as a genealogical tree of living beings.

2. MORPHOLOGICAL EVIDENCE.—Certain facts are inexplicable on the theory of special creation, while they are naturally explained on the theory of descent. The common morphological plan of construction exhibited by the members of a systematic group, such as a genus, a family, or a class, is of this nature. It extends in a sense to all organisms as shown in the cellular structure and the nature of protoplasm. The great groups of the Bryophyta, Pteridophyta, and Gymnosperms, with all their morphological differences, are essentially similar in the course of development and alternation of generations, and in the construction of their sexual organs. On the other hand, the theory of evolution may explain the unexpected occurrence of certain features in a group when the plan of construction would not have led us to anticipate them (*e.g.* the spermatozoids in the pollen-tube of the Cycadeae).

The numerous homologies and analogies between the organs of plants (p. 155) all point to such a phylogenetic transformation as is required by the theory of descent. The organs of one and the same organism are frequently homologous, *i.e.* morphologically equivalent, in spite of their diverse structure and functions. For example, thorns and tendrils are "transformed" leaves, stipules, stems, or roots; the cotyledons, scale-leaves, bracts, sepals, petals, stamens, and carpels of a plant are all "transformed" foliage leaves. All these metamorphoses of organs have evidently taken place during the phylogenetic development. Organs of different species, that appear completely different and perform different functions, may also prove on morphological investigation to be homologous. On the other hand they may, in spite of agreement in form and function, prove to be based on surprisingly distinct fundamental forms and thus be only analogous.

In the same way reduced functionless organs found in some plants have been derived from plants in which the corresponding organs are still well formed. In the family of the Scrophulariaceae (Fig. 226) the number of stamens ranges from five in *Verbascum* to two in such forms as *Calceolaria*; in the genus *Scrophularia* one stamen of the five is present in a reduced condition, while this stamen is wanting in *Digitalis*; in *Gratiola* two fertile and two reduced stamens are present, in *Veronica* two fertile stamens only, and in *Calceolaria* only two half-stamens. Useless reduced organs are difficult to understand on the theory of special creation.

Occasionally in a plant an unfamiliar character appears which can only be regarded as a reversion (ATAVISM, cf. Fig. 550) to a long-lost feature of its ancestors; examples are afforded by the occasional fertility of reduced stamens or the appearance of reduced or fertile stamens in positions where fertile stamens were present in the ancestry.

The similarity of the embryos of very different organisms, which is most strikingly shown in the animal kingdom, is a further indication of genetic relationship. So also is the fact that occasionally the embryos are more highly organised than the mature organism (in some reduced organisms, *e.g.* many parasites). The juvenile leaves on the seedlings of some plants which are adapted to extreme conditions of life may resemble the ordinary leaves of less specialised species of the same genus (*e.g.* in *Acacia*, Fig. 136). Not infrequently a species repeats more or less completely in its ontogenetic development what we assume on other grounds to have been the course of its phylogenetic development (BIOGENETIC LAW).

3. EVIDENCE FROM GEOGRAPHICAL DISTRIBUTION.—Geographical limits which hinder free migration (*e.g.* high mountains and seas in the case of land-plants and masses of land in the case of marine organisms) stand in striking correspondence with differences in the fauna and flora of particular habitats, countries, continents, or oceans. The assemblages of organisms found in two continents differ as regards their families, genera, etc., in proportion to the degree of present and former isolation because the forms in each region have continued their phylogenetic development independently. The easier the exchange of forms between two regions the more numerous will be those which are common to both. It is a general rule that the inhabitants of any region are most closely related to those of the nearest region from which migration may be assumed, on geological and geographical reasons, to have taken place. This holds, for example, for the Cape Verde Islands and the African mainland, and for the Galapagos Islands or Juan Fernandez and the neighbouring regions of America. The more a habitat, such as an island, is isolated from the rest of the world the richer will it tend to be in peculiar forms (ENDEMISM). These often differ only slightly from other non-endemic forms from which they have evidently originated in the present habitat, though further dispersal has been impossible (progressive endemism). Others are remains of what were at one time

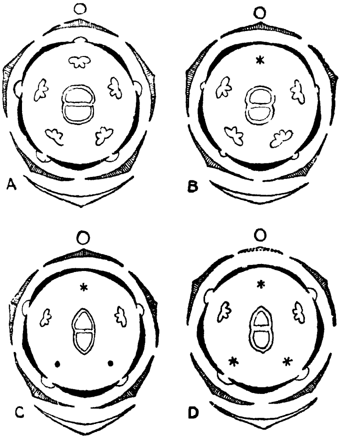


FIG. 226.—Floral diagrams of Scrophulariaceae. *A*, *Verbascum nigrum*; *B*, *Digitalis purpurea*; *C*, *Gratiola officinalis*; *D*, *Veronica Chamaedrys*. The sterile stamens are represented by black dots, and the position of completely aborted stamens by crosses. (*D* after EICHLER.)

more widely distributed forms and have no special relationship to others in the region; such forms may be very ancient and indicate an extinct flora (relic endemism).

4. PALAEONTOLOGICAL EVIDENCE.—Palaeontology shows that in the history of the earth species have become extinct and others appeared; that not infrequently the forms in successive geological strata can be arranged in series showing progressive organisation; and that the groups which are regarded as most highly organised appeared relatively late in the history of the earth (*e.g.* the Angiosperms in the Cretaceous period). It has also made us acquainted with extinct intermediate types between genera, families, and classes. That such cases are not more frequent evidently depends on the incompleteness of the geological record. In Botany the most important of these synthetic groups is that of the Pteridospermeae or Cycadofilices, which are plants of the Carboniferous period connecting the Ferns and the Cycadeae; they have leaves like the former but seeds like the latter, while anatomically they present resemblances to both.

5. DIRECT EVIDENCE OF THE VARIABILITY OF SPECIES.—All the preceding sources of evidence gain in significance from the direct observation of the inconstancy of some species. Careful observation establishes the appearance, both under natural conditions and, more frequently, in cultivation, of inheritable deviations which would have the systematic rank of varieties or species. It has also been possible in various ways to experimentally produce new forms the characters of which are inherited. The importance of such observations is that they give some insight into the problem of the formation of species and the origin of new morphological characters (cf. pp. 325 ff.). All observations have so far shown that the inheritable changes in organisms may concern this or that character, may be larger or smaller, and are irregular in origin. This serves to elucidate the great variety in organic forms. These abrupt changes may be harmful, indifferent, or useful to the organism. If they are so injurious that the life of the organism is scarcely possible, the variety will disappear as quickly as it originates (*e.g.* seedlings that have lost the power of forming chlorophyll). To what extent such inheritable changes arise under the influence of external conditions has yet to be determined in particular cases.

B. The Origin of Adaptations.—Since the acceptance of a theory of evolution it has been evident that the origin of the ADAPTIVE CHARACTERS of organisms called for special explanation. The recognition that living beings vary in all directions does not afford insight into the striking fact that organisms are in many ways adapted to their environment, and organs more or less adapted to their functions, while the reactions of the organisms are beneficial. This condition of adaptation or inherited adaptedness must in some way have originated phylogenetically. As to how it arose, observations and experiments have so far given no direct answer. Explanations have been sought in a different way, the two most important hypotheses being known as Lamarckism and Darwinism.

1. **Lamarckism** (^{113}).—This hypothesis starts from the fact that some organisms assume a different form according to the surroundings in which their germ cells develop to the mature organism, without losing the power of developing differently in another environment. Thus there are plants which can live both on land and in the water (amphibious), assuming different forms according to the environment. When grown on land they have the form and internal structure of typical land-plants; when cultivated in water they resemble typical aquatic plants. Some plants under dry conditions of cultivation produce xeromorphic characters, while when grown in moist air they are hygromorphic. This power of reacting to different environments by the development of different characters is known as the capacity of modification. Such MODIFICATIONS (cf. p. 324) are not inheritable in the sense that the seeds of, for example, an amphibious plant which has developed in water to a water-plant will produce the aquatic form if they are sown on land. On the contrary, the land-form is always produced on land and the aquatic form in water whether the seeds have been taken from the one form or the other.

These influences of the environment have been regarded as direct adaptations on the part of the plant which has the power of thus modifying itself. The power has further been attributed to the organism of responding by a useful reaction to every external influence, even to those not met with under natural conditions. Such a power of adaptation would apply to new functions as well as to external factors; the need of an organ would bring about its formation. How this would be possible is, however, far from clear. Further, it is difficult to conceive that the organism should react usefully in anticipation of particular external factors. As a matter of fact we not uncommonly meet with reactions to new unaccustomed stimuli which appear quite indifferent or even harmful. Thus the tentacles of *Drosera* become curved at a high temperature just as if they were in contact with an insect. Leaves cut off from a plant may continue to live for years by producing roots even when they are unable to form shoots. When there appears to be direct adaptation to various stimuli (*e.g.* water, light, air, shade, etc.), to which particular organisms are exposed in their habitats, the result may be otherwise explained. It may be assumed that such organisms already possess the capacity or the factors which enable them to follow this or that course of development according to the external conditions. The external conditions would not produce the factors but only determine their becoming manifest or not. How these factors have historically come about, and why some organisms possess them and others not, why, for example, only some plants are adapted to live in water as aquatic plants or as land-plants on the land, remains still unexplained.

It is further assumed by Lamarckism that every modification, especially those resulting from external factors or the needs of the organism, is inheritable, or at least can become inheritable in the course of time. Thus when a plant has been for generations directly adapted to aquatic life, to life in the shade, or at the expense of another organism, the acquired peculiarities of structure gradually become fixed, *i.e.* they also appear when the occasion for them is no longer present. Nothing is, however, known of the inheritability of those effects of external conditions that have been termed modifications above.

2. **Darwinism** ($^{112, 114}$) starts from the fact that organisms with almost any properties, useful, indifferent, or injurious, can arise by inheritable variation. Nearly every living being produces during its individual existence so many germs that were all to grow the whole earth would in a short time be overpopulated. That so few descendants of an individual survive is due to many being destroyed at all stages from the germ-cell onwards. They are overcome in the STRUGGLE FOR EXISTENCE with the environment, in which other organisms of the same or different species are included. Were all the offspring alike, accident only would decide which should survive, and such accidents do play a great part. Since, however, inheritable differences occur among the offspring, those individuals will as a rule be favoured in the struggle for existence which by their peculiarities are capable of maintaining themselves, or are more capable than the others in the particular situation to which chance has brought them. Thus a process of selection (NATURAL SELECTION) comes about. If, further, the selected variants hand on their properties to their descendants, and the variation and the struggle for existence is repeated, the process must lead to the selection of still better adapted forms. Since, however, all with injurious qualities sooner or later disappear, those that remain are better adapted than those that perish. Usefulness (adaptedness) which was not explained by Lamarckism (where the useful capacity of reaction in relation to new conditions of the environment was assumed) comes about according to Darwinism from the preservation of new inheritable properties which contribute to the success of the organism in the struggle for existence. It is in this that the great advance made by DARWIN'S theory, as compared with Lamarckism, consists. The assumptions of Darwinism still leave various difficulties to be overcome, especially when the gradual origin of highly differentiated organs with many adaptive features has to be explained.

DIVISION II

PHYSIOLOGY

DIVISION II

PHYSIOLOGY (¹)

THE object of Physiology is to describe the phenomena of life, to study their dependence on external factors, and, so far as possible, to trace them back to their CAUSES. Physiology, like Chemistry and Physics, is concerned with inquiries into the causes of what takes place. It must, however, also take into consideration the significance to the organism of what happens. In its methods as well as in its problems Physiology agrees with Physics and Chemistry; its methods are EXPERIMENTAL.

There is no fundamental distinction between the vital phenomena of animals and plants. This is not surprising, since plants and animals are only morphologically distinct in their more advanced representatives. In the physiological sphere it becomes more and more clear, as investigation proceeds, how similar the course of life in the two kingdoms is. The physiology of organisms is thus really a single subject. A text-book of botany has evidently only to give an account of the physiology of plants, but, where this is useful, analogous phenomena in the animal kingdom will be mentioned.

In some respects the behaviour of the living plant does not differ from that of non-living bodies. In spite of the large amount of water which it contains, the plant is as a rule solid, and has the physical properties of such a body. Weight, rigidity, elasticity, conductivity for heat, and electricity are properties of the organism as they are of lifeless bodies. However important these properties may be to the existence and the life of the plant, they do not constitute life itself.

The ESSENTIAL PHENOMENA OF LIFE are at first sight strikingly different from the processes met with in non-living bodies. So long as the organism is actively living, an unbroken chain of changes can be recognised in it which are exhibited in the three following ways:

(i.) An organism does not consist of the same unchanged material, even when no further growth in size is taking place. While its external form remains constant, progressive changes go on internally. New substances are taken up from without, are transformed within the plant, and are again given off from it. The organism has a METABOLISM.

(ii.) As a rule, however, metabolism does not proceed so that the absorption and giving-off of material are equal, but more is absorbed than is given off. The mass of the organism is increased, it GROWS. The organism by changes of its form assumes quite definite shapes, which follow in regular order. It passes through a DEVELOPMENT which leads sooner or later to the production of new organisms or daughter-individuals; REPRODUCTION takes place. Growth, development, and reproduction are processes highly characteristic of living beings.

(iii.) Lastly, organisms exhibit powers of MOVEMENT; they either change their positions bodily, or they bring larger or smaller parts of their bodies into other positions. Since inorganic bodies and dead organisms may exhibit movements, it is only the kind of movement and the means by which it is brought about that are characteristic of living beings.

In nature the three processes mentioned above, metabolism, development, and movement, usually go on simultaneously. Metabolism without movement of the substances concerned is impossible; development is bound up with metabolic changes and with movements; and, lastly, movements cannot occur without metabolism and without change of form. Nevertheless, we may for descriptive purposes consider the three processes separately, and thus divide Physiology into the following sections:

(1) The study of metabolism or chemical physiology, which may also be termed the physiology of nutrition.

(2) The study of development or the physiology of form and changes of shape.

(3) The study of movement and changes of position.

Before passing to the consideration of these three groups of vital manifestations, it is necessary to become acquainted with some important general results of physiological investigation.

1. The manifestations of life are connected with the protoplasm. The structure and organisation of this determine what happens in the organism and give it the characters of a living being. For the appearance of vital manifestations it is important that the protoplasm should be in the proper condition. As soon as it is dead these cease. But living protoplasm itself can occur in two distinct states and be either ACTIVELY LIVING or in a condition of LATENT LIFE. Protoplasm in the latent condition is met with, for example, in resting seeds. In these even the most delicate methods of measurement may fail to demonstrate any indications of life, but the protoplasm is not dead and can at any time pass into the condition of active life. For this it is only necessary to change the external conditions, for instance, to supply the seed with water. Whether the protoplasm is in the one

or the other state depends on the external conditions Protoplasm can only carry on its activities by continual interaction with the environment. It requires to obtain material for its nutrition from this, and also requires a supply of energy since the vital phenomena involve the performance of work in the sense of mechanics.

In considering the external factors that are of importance for the life of a plant, a distinction must be drawn between the necessary and the inessential factors. Indispensable conditions of vital activity are a certain temperature and the presence of certain substances, as well as the absence of others that act injuriously or fatally (poisons). On the other hand, light is not in such a general sense a necessary condition for life. Some plants require direct sunlight, at least for their aerial organs, while others avoid this and seek the shade (shade-plants); others can pass through their whole life-history in complete darkness.

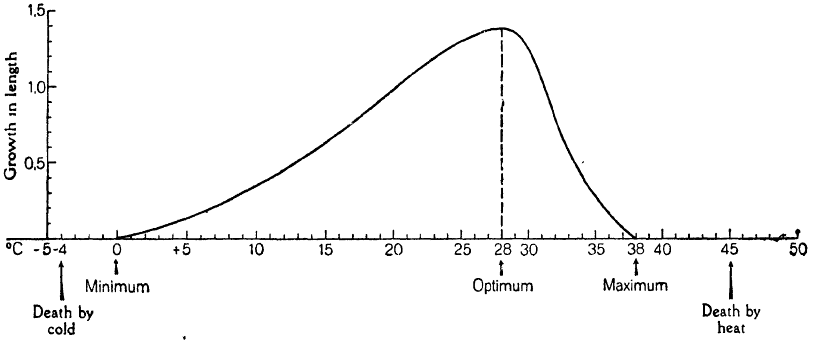


FIG. 227.—Growth in length at various temperatures (optimum curve).

Not merely the presence of the essential factors but their degree is of importance, for only within certain limits do the external factors permit of active life. The growth of a plant is one of its most striking vital manifestations. Taking this as an example, we may inquire how it is affected by various temperatures. A growing plant is placed for certain periods, say of two hours, under different temperatures and the growth which it makes in these periods recorded. To obtain a general survey the results are expressed graphically, the abscissæ marking the different temperatures and the ordinates the amount of growth at each temperature (Fig 227). The curve begins at a temperature that is usually in the neighbourhood of 0° C.; this is the MINIMUM. Below this temperature no growth is found to take place. On proceeding to successively higher temperatures the curve is found to rise but it does not do this indefinitely; at a certain temperature, the OPTIMUM, the greatest growth takes place. From this onwards the curve falls to the MAXIMUM beyond which again no growth is found to take place. Such a curve is called an OPTIMUM CURVE and the three points, minimum, optimum, and maximum, its CARDINAL POINTS. Outside this range two other points can be established. When the growing plant is placed at temperatures below the minimum or above the maximum, no growth is to be recognised, but the plant is not at once killed. Only after some two hours at a temperature above the maximum does death take place. Too high a temperature thus leads to death from heat and correspondingly too low a temperature to death from cold. These two points can be marked as DEATH-POINTS on the curve.

The three cardinal points and the two death-points for the temperature curve are by no means constants. They differ for particular organisms and particular vital phenomena. Further, they change with the duration of the influence of the factor, and they depend on the condition of the plant and on the other external factors to which it is exposed.

Thus plants behave very differently as regards the two death-points. While, for example, some tropical plants are killed even at temperatures above 0° C., other plants can endure very low temperatures. *Cochlearia fenestrata*, which occurs in Northern Siberia, endures a temperature of -46° C. without injury, and some forest trees can stand even -60° C. The resistance of lower organisms to extreme cold is noteworthy. It has been shown that Diatoms can endure for a long time a temperature of -200° C. What holds for death from cold applies also to death from heat. While most plants are killed by temperatures far below the boiling-point of water some Cyanophyceae can endure the very high temperatures (up to 93° C.) of certain hot springs.

Air-dry seeds and spores can withstand temperatures of 100° C. and more, though in the water-soaked condition they are killed by a temperature of 50°-55° C. The succulent parts of some plants are killed by immersion for 10 minutes in water at 45°-46°, while in air they are killed only by 10 minutes at 51° C. The death-points for temperature may be different for young and old plants (^{2}).

What has been said above as regards temperature applies also to all other external conditions. It holds for both necessary and inessential factors and even for factors acting within the plant, which will be considered later. The optimum curve and what has been said about it applies to all these cases, so that it can be regarded as a fundamental curve in physiology. Too much or too little is injurious with respect to all factors, though only a few examples can be given here.

By increase of the INTENSITY OF LIGHT any cell can be killed; in different cases the action of the light may be either mainly chemical or mainly thermal. Many Bacteria are killed even by bright daylight; on this depends the important hygienic effect of light in houses and dwelling-rooms.

The need of light not only changes from one species of plant to another, or from individual to individual, but the optimum effect of light may change for the same individual as it develops. Many of the cultivated plants of the tropics, *e.g.*

Coffee and Cocoa, require shade when young, and need to be at first protected by shade-giving trees (species of *Albizzia*, *Musa*) planted for this purpose. When older they bear, or even require, exposure to the full tropical sun.

The optimum curve holds also for FOOD-MATERIALS and in a certain sense also for POISONS. With too little of the former a starved condition results, while too much has a poisonous effect. This influence thus resembles that of poisons ; very low concentrations of the latter have already exceeded the maximum.

The influence of WATER is especially important. In the case of most plants too little water soon results in wilting, which is followed by drying up. While the majority of plants are very sensitive to a deficiency of water others have a great power of enduring this. Thus, Lichens and Mosses, which live on rocks, on the bark of trees, and in similar situations, some Algerian species of *Isoëtes* and *Selaginella lepidophylla*, a native of the dry high plateau of Central America, can be thoroughly air-dried without being killed.

Death does not necessarily at once result when the maximum or minimum for external factors is overstepped. The organism frequently passes into the condition of latent life, mentioned above. It is often difficult to decide from inspection whether an organism is in this state or is already dead ; only experiment can decide in any particular case.

Frequently also the latent condition on exceeding the maximum or minimum does not apply to all the vital manifestations of the protoplasm ; at first, only some of these may be suspended, while others that have a different maximum continue.

The striking regularity in the behaviour of protoplasm which is expressed in the optimum curve evidently depends on its great LABILITY TO THE MOST VARIOUS EXTERNAL FACTORS. This is specially characteristic of protoplasm. External influences act on the protoplasm in such a way that, as has been seen, it may be so irreparably altered as to be no longer functional ; it is destroyed by a kind of coagulation and is dead. It must be assumed that the latent protoplasm has been modified in some way whereby the manifestations of active life are arrested. The changes in the latent condition, in contrast to the irreversible changes of death, are reparable or reversible.

In this connection it must be noted that the entry into latent life is not always the result of overstepping the maximal or minimal limits for external factors. It is often determined by inner causes, as is seen, for example, in the development of spores, seeds, tubers, etc.

The optimum curve is so distinctive for the living substance, and thus for the whole organism, that it serves as the most important criterion to determine whether a process in an organism is vital or not. It is, in a certain sense, the graphic representation of the mathematical regularity according to which any particular factor acts causally upon a particular vital process. It thus becomes an important question whether its particular form is peculiar to the organism and is not met with in the inorganic world. Investigation has shown that something of the same kind is met with in non-living nature, especially in colloidal substances, showing that in this respect there is no essential difference between living and non-living bodies. Thus the ascending branch of the optimum curve, which was established above for different temperatures, is characteristic of almost all chemical reactions. Strictly speaking it is only the descending branch of the curve which is noteworthy. This is, however, readily explained by the great lability of the protoplasm, in which arresting influences, that have been accumulating before the optimum, preponderate at the maximum and beyond this. There are in non-living nature also numerous processes which are slowed off by a particular amount of a factor which affects them. While this characteristic method of reacting is not exclusively distinctive of living beings, no other substance is known which is so labile to all possible alterations in external factors as is protoplasm.

2. The living substance works according to the laws of Physics and Chemistry and employs in all the manifestations of its life the materials and the energies of non-living nature. Neither a peculiar "vital-element," nor a special "vital force," peculiar to the organism and underlying the process of life, has so far been demonstrated. What happens, in so far as it concerns material, is only the transformation of non-living matter into the organic chemical compounds specially characteristic of the organism; and, so far as energy is concerned, only the transformation of non-living potential and kinetic energy into the potential and kinetic energy peculiar to the living body. Whether, however, life is susceptible of a purely physico-chemical explanation as the mechanistic theory holds, or whether at least the way in which the changes in the living being proceed is not different from anything in non-living nature (vitalism) is a question that cannot at present be decided. Analytic methods of investigation have hitherto shown that the organism, at least in very many cases, employs the causal laws of Physics and Chemistry just as mechanistic theory would desire and expect. Whether, in spite of this, there will remain an inexplicable residuum cannot yet be said; it seems at the moment doubtful whether it would be possible in the future to recognise such a residue, owing to the great complexity of the vital processes.

III. When we look beyond the characteristic dependence of vital processes on the external world, as shown by the optimum curve, there remains much that is mysterious and completely unexplained in them. This is shown especially clearly by two remarkable characteristics of living beings, their IRRITABILITY and their CAPACITY FOR REGULATION.

(a) Irritability.—In the reactions of the organism the connection between the causal influence and the effect induced by it is not so apparent as it is in chemical or physical processes. This depends on the part always taken by the protoplasm, so that the reaction observed is not the direct effect of an external cause, but a very indirect result. Further, according to the condition of the protoplasm, the same factor may produce different effects. An example will make this clear.

If the free end of a flexible rod is placed horizontally, it will bend downwards to a definite point as the result of its weight. A part of a plant will behave similarly, and if dead, as for instance a withered stem, will remain in the position it thus assumes. If, however, a living growing stem has been used in the experiment it will exhibit an effect of gravity which is very surprising in comparison with the purely physical effect. The growing portion of the stem curves, and by its own activity becomes erect again; it thus moves against the force of gravity. If the experiment is made with a tap-root, this will curve vertically downwards much further than its own weight would cause it to do. A rhizome (*e.g.* of *Scirpus*), on the other hand, will place its growing tip horizontally when it has sunk by its own weight out of the horizontal plane In these three experiments the physical conditions are the same. The weight of the earth acts on a horizontally-placed portion of a plant. The results in the three cases are as different as possible.

The explanation of this remarkable behaviour of the plant is to be sought in the fact that, while to begin with the external influence has the same effect as it would have on an inorganic structure—in the particular example the force of gravity gives rise to compression—this primary physical change then liberates inner activities of the plant so that the external factor appears to have acted as a liberating force. Such relations become clearer if the organism is compared with a mechanism. The connection between the light pressure of the finger on the trigger of a gun and the flight of the bullet is not a simple one. The pressure first liberates a trigger; the energy thus obtained drives the hammer on to the percussion-cap; this explodes and causes the powder to explode; the gases liberated by the explosion force the projectile from the barrel. It is clear that the force of the hammer bears no relation to that of the pressure of the finger of the marksman, and there is just as little connection between the amount of force generated by the expansion of the powder and that exerted by the hammer of the gun. There are energies present, those of the trigger and powder, which are set free. Such LIBERATIONS OF ENERGY, especially when they follow in order and constitute a chain of processes, are met with in all vital phenomena. They are, it is true, not so simple or comprehensible as in the case of mechanisms, since the whole process goes on in the protoplasm. Such liberations of the potential energy accumulated in the living substance and its transformation into kinetic energy are known as PHENOMENA OF IRRITABILITY. The factor which starts them is termed a STIMULUS.

Just as the action of a machine is only comprehensible when its construction is known, a knowledge of the external form and internal structure of the plant is a necessary preliminary to its physiological study. It has been seen, however, that it is not possible to understand the function from the structure to the same degree in the case of the plant as it is in that of a machine. In the organism we are concerned not with the mechanical interaction of parts but with a succession of chemical reactions.

(b) Capacity of Regulation.—The study of machines not only assists in the comprehension of a liberating stimulus but further renders clear the second widely-spread property of organisms, *i.e.* their regulative power. As in a machine the speed may be automatically maintained at a particular level, so in numerous processes in a plant there is an element which controls the result both as regards quality and quantity. Though self-regulated processes are not wanting in the inorganic world, they do not occur abundantly as they do in the organism. ON THIS ACCOUNT THE POWER OF REGULATION MAY BE REGARDED, TOGETHER WITH THE IRRITABILITY, AS A SPECIALLY IMPORTANT CHARACTERISTIC OF LIVING BEINGS.

SECTION I

METABOLISM (3)

I. The Chemical Composition of the Plant (4)

Any consideration of the metabolic changes in the plant requires a knowledge of its chemical composition. This is studied by chemical methods.

Water and Dry Substance.—Some insight into the composition of the plant can be obtained without special means of investigation. Everyone who has dried plants for a herbarium knows that the plant consists of water and dry substance. By means of weighing it is easy to show how large is the proportion of water in the total weight of the plant. For this purpose it is not sufficient to expose the plant to the air, for when air-dried it still retains a considerable proportion of water, which must be removed by drying in a desiccator or at a temperature of slightly over 100° C. It can thus be ascertained that the proportion of water is very considerable; in woody parts some 50 per cent, in juicy herbs 70-80 per cent, in succulent plants and fruits 85-95 per cent, and in aquatic plants, especially Algae, 95-98 per cent of the weight of the plant consists of water.

Ash.—While we can thus distinguish by drying between the water and the dry substance of the plant, we are able by burning to distinguish between the combustible or ORGANIC MATERIAL and the incombustible substance or ASH. The fact that the plant leaves an ash is evident in the burning of wood or in the smoking of a cigar; the microscope further shows that even minute fragments of cell-wall or starch-grains leave an ash on burning.

When the amount of ash contained in the various organs of diverse plants is determined, the percentage which this forms of the dry weight shows a wide range. This will be clear from the first column of the following table. The separate organs of the same plant differ in this respect; for example, the straw of Rye or of the Pea contains more ash than the seeds. Leaves tend to have a larger proportion of ash than stems.

The constituents of the ash also vary according to the nature of the soil and other external influences. On the other hand, distinct species may accumulate different quantities of mineral substances, even when exposed to the same external conditions.

Plants.	Ash in 100 parts of dry solid matter.	100 parts of ash contain									
		K_2O	Na_2O	CaO	MgO	Fe_2O_3	Mn_3O_4	P_2O_5	SO_3	SiO_2	Cl
Rye (grain) . .	2·09	32·10	1·47	2·94	11·22	1·24	..	**47·74**	1·28	**1·37**	0·48
Rye (straw) . .	4·46	22·56	1·74	8·20	3·10	1·91	..	**6·53**	4·25	**49·27**	2·18
Pea (seeds) . .	2·73	43·10	0·98	**4·81**	7·99	0·83	..	**35·90**	3·42	0·91	1·59
Pea (straw) . .	5·13	22·90	4·07	**36·82**	8·04	1·72	..	**8·05**	6·26	6·83	5·64
Potato (tubers).	3·79	60·06	2·96	2·64	4·93	1·10	..	16·86	6·52	2·04	3·46
Grape (fruit). .	5·19	56·20	1·42	10·77	4·21	0·37	..	15·58	5·62	2·75	1·52
Tobacco (leaves)	17·16	29·09	3·21	36·02	7·36	1·95	..	14·66	6·07	5·77	6·71
Cotton (fibres) .	1·14	36·96	13·16	17·52	5·36	0·60	..	10·68	5·94	2·40	7·60
Spruce (wood) .	0·21	19·66	1·37	33·97	11·27	1·42	**22·96**	2·12	2·64	2·73	0·07

While the majority of the more common elements occurring in the earth are found in the ash of plants, only a few elements are present in sufficient amount to be quantitatively estimated. These are the non-metals Cl, S, P, Si, and the metals K, Na, Ca, Mg, and Fe.

The above table gives some information as to the amount and distribution of these substances in a number of cultivated plants.

The difference brought out by the table in the proportions of phosphoric acid and of silica and lime contained in Rye and Pea seeds, as compared with the amounts of the same substances in the straw, is worthy of notice. The Potato contains much K_2O and little CaO, while the wood of Spruce shows the opposite condition.

In the preceding table the figures do not express absolutely constant proportions, as the percentage of the constituents of the ash of plants varies according to the character of the soil. It is perhaps well to make clear that the oxides as given in the table are mostly formed in the process of incineration. In the living cell the metallic elements are present as salts, especially of organic acids.

Organic Substance.—The organic substance consists in the first place of the elements H, O, N, and C. On complete combustion it is transformed into volatile compounds—carbon dioxide, water, ammonia, or free nitrogen. Some of the elements found in the ash were contained in organic compounds in the plant. Chemical analysis is not needed to show that the plant contains carbon in a combined form. Every burning log or match shows by its charring that it contains carbon. The examination of a piece of charcoal in which the finest structure of the wood is retained, shows further how uniformly the carbon is distributed in the plant, and how largely the substance of the plant consists of this element. Accurate weighing has shown that carbon constitutes about one-half of the dry weight of the plant. Some of the compounds of carbon found in plants are non-nitrogenous (*e.g.* carbohydrates, fats, organic acids), while others contain nitrogen (*e.g.* albumen, alkaloids). The main facts regarding the organic compounds found in the plant have been given in the morphological part when treating of the cell (pp. 14, 26 ff).

Source of the Materials.—There are thus only the following thirteen elements found in considerable quantity in the plant:

H, Cl, O, S, N, P, C, Si and Na, K, Mg, Ca, Fe.

When the plant is growing their amount is continually increasing in the plant, and they must therefore be continually absorbed from without, from the soil, water, air, or from other organisms.

As a rule, only gases and liquids can enter the plant; solid substances have to be brought into solution before they can pass through the firm cell-walls. When, however, cell-walls are absent, as in the *Flagellates* and Myxomycetes, the naked protoplasm is able to surround and thus to absorb solid particles (animal nutrition).

The chemical composition of animals is essentially similar to that of plants. The absorption of food in animals takes place by means of the digestive system. The contrast is, however, not so great as appears at first sight, for as a rule the food materials are converted into a fluid condition before they are absorbed by the cells.

II. The Nutrient Substances obtained from the Soil

Chemical analysis ascertains all the elements present in the plant. It does not, however, show whether these substances are utilised by the plant nor whether the substances always present in the ash are necessary for nutrition and are thus to be regarded as food-materials. Such questions can only be decided experimentally. The first problem is to determine which substances obtained from the soil by the plant are essential, *i.e.* necessary, constituents of its food. To decide this, careful cultural experiments with chemically controlled nutrient soil are requisite.

This conclusion can be reached in two ways. The first method is to cultivate the plant in an artificial soil composed of insoluble substances such as platinum, pure carbon, pure quartz, with which the substances to be investigated can be mixed. The second method, that of WATER-CULTURE, is more convenient. Many plants are able to develop their root-system in water instead of in the earth. It is thus possible to add to the water the elements found in the ash in various combinations, and so to ascertain which elements are necessary and which superfluous. As Fig. 228, *I*, shows, the plant (Buckwheat) succeeds well in such a food-solution if of suitable composition; it can form roots, shoots, flowers, and fruits, and increase its dry weight a hundredfold or a thousandfold, just as if it were growing in the soil. In distilled water, on the other hand, while the plant begins to grow normally, the growth soon ceases entirely, and only a very dwarfed plant is produced.

Culture-solutions of various composition are used (5). KNOP's solution contains—water 1000, calcium nitrate 1, magnesium sulphate 0·25, acid potassium phosphate 0·25, potassium nitrate 0·25, and a trace of ferric chloride. The solution of v. D. CRONE, with almost completely insoluble compounds of phosphoric acid and iron, appears in some cases to give better results (water 1000, potassium nitrate 1, potassium sulphate 0·5, calcium sulphate 0·5, potassium phosphate 0·25, ferrous phosphate 0·25). In addition to these a number of other combinations of salts have been tested.

From such water-cultures it results that the typical green land-plant succeeds satisfactorily if supplied with the elements K, Ca, Mg, Fe, and H, O, S, P, N, if in addition O and C (the latter as carbon-dioxide) are available in the atmosphere. There are thus in all ten elements which must be regarded as indispensable food-materials. Of these the seven which remain after excluding H, O, and C concern us here, since the plant obtains them as nutrient salts from the soil or water. Six of these seven are found in the ash, while the nitrogen escapes on combustion in the form of volatile compounds. That these seven elements are completely indispensable is shown by the fact that if a single one is wanting its loss cannot be made good by an excess of the others, or by the presence of a related element.

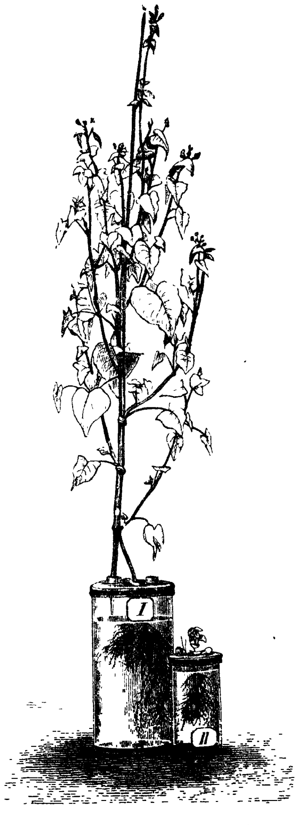


FIG. 228.—Water-cultures of Buckwheat (*Fagopyrum esculentum*). *I*, In nutrient solution containing potassium; *II*, in nutrient solution without potassium. Plants reduced to same scale. (After NOBBE.)

Thus, for example, potassium cannot, as a rule, be replaced by sodium, lithium, or rubidium. Lower organisms (Algae, Bacteria, Fungi) are able to do without Ca. The absence of a single necessary element is shown either by the feeble and dwarfed development of the plant (Fig. 228, *II*, absence of potassium) or by characteristic changes in the plant. The best known of these is the effect of absence of iron, in which case the plant does not become green (chlorosis). Injurious effects of poisoning are shown when calcium is lacking.

More accurate consideration shows that it is not correct to speak of these definite elements as the food-materials of the plant. Just as a mixture of the elements H and O is not a substitute for water, it is not sufficient to supply the plant with the elements contained in the nutrient salts either as elements or in any of their combinations. Thus metallic potassium or pure sulphur are of no use. The plant requires particular salts or, since these in part dissociate in water, particular ions. Necessary kations are K^+, Ca^{++}, Mg^{++}, Fe^{++} (or Fe^{+++}), while SO_4^{--}, $H_2PO_4^-$, and NO_3^- are necessary anions. While phosphorus and sulphur can only be utilised in these combinations, the nitrogen can also be obtained, although not always so usefully in the form of the kation NH_4^+.

Numerous investigations in recent years have made clear the further important point that a certain degree of acidity of the food-solution or the soil is necessary for the normal development of a plant.

The acidity depends on the proportional number of H- or OH- ions present in the liquid. If these are present in equal numbers the liquid is neutral; if the H ions preponderate the reaction is acid, and if the OH ions are in the majority it is alkaline. It is customary to record the acidity by means of the number of H ions present in unit volume, and, for certain reasons, to denote it by the negative logarithm of this number; this is termed the pH value of the solution. For a neutral solution $p\mathrm{H}=7$; for acid solutions its value lies between 1 and 7, and for alkaline between 7 and 14 (6 and 7).

If various plants are cultivated in soils or culture-solutions with different reactions it becomes evident that some plants succeed better when the solution has an acid reaction, while others do better in solutions that are neutral or weakly alkaline. This is shown by the following table, which is based on determinations by a special method of the fresh weight of plants all grown in the same normal food-solution. This has been given different pH values.

Reaction of Food Solution.	3·5	4·5	5·5	6·5	7·5	8·0
Aira flexuosa . .	4	**4·5**	3·0	1·7	dead	dead
Senecio sylvaticus .	21·0	**25·0**	15·0	5·0	1·0	dead
Tussilago farfara .	dead	7·0	30·0	**35·0**	2·1	1·0
Hordeum distichum.	3·0	45·0	86·0	**88·0**	10·0	4·0
Elodea canadensis .	dead	dead	2·6	3·3	4·4	**6·5**

A special case of this adaptedness to a particular reaction of the soil is afforded by calciphilous and calciphobous plants. The calciphobe plants require calcium for their normal nutrition just as do the calciphilous ones; what the calciphobous plants cannot endure in habitats rich in lime is the alkaline reaction of the soil (8).

Just as is the case for C, N, H, and O, some other elements of nutrient salts enter into the chemical composition of important materials in the plant, *e.g.* S. and P in albuminous compounds and Mg in chlorophyll. It is possible that other metallic elements enter into necessary organic compounds. What is certain is that they also play a quite different, physico-chemical rôle. The SALTS MAINTAIN THE COLLOIDAL PROTOPLASM IN ITS NORMAL CONDITION AND ENTER IN A REGULATING FASHION INTO ALL PHYSIOLOGICAL PROCESSES.

The method of water-culture has not only shown the necessity for certain salts, but also that many substances, especially sodium, chlorine, and silicon, which the plant usually absorbs and sometimes accumulates, are not essential.

Even in HALOPHYTES, in which it is present in greatest quantity, SODIUM is not indispensable. These plants live in soils rich in sodium chloride not because this substance is necessary to them but because they bear it better than other plants do. The concurrence of these in such localities is thus prevented. The characteristic succulent construction of halophytes (Fig. 188) is more or less completely lost in the absence of common salt. Sodium appears, however, to be indispensable to the Diatoms and some Seaweeds (8).

SILICON is not indispensable to *Equisetum* and Grasses which contain considerable quantities of SiO_2; on the other hand, it is requisite to the Diatoms, the cell-walls of which are almost entirely composed of silicic acid, and owe their permanence to this. The cell-walls of Diatoms form considerable geological deposits of siliceous earth or kieselguhr. ALUMINIUM (9), while generally distributed in small quantities, is only absorbed in considerable amount by a few plants (*e.g.* species of *Lycopodium*). According to STOKLASA it is indispensable to water-plants. Although scarcely a trace of IODINE can be detected by an analysis of sea-water, it is found, nevertheless, in large quantities in seaweeds, so much so that at one time they formed the principal source of our supplies of this substance. Whether it is essential to these plants is not known.

The substances which, as culture experiments show, are not indispensable for the life of the plant may, however, be of use and of advantage in growth. For example, Buckwheat and other plants flourish better when supplied with a chloride, and the presence of silica is advantageous as contributing to the rigidity of the tissues. It has also been found that the presence of certain substances which are not of direct use may inhibit the poisonous action of other substances some of which are necessary.

It is known that salts are necessary for animals as well as for plants, but the particulars are not clearly ascertained. Probably they require the same elements as plants do with the addition of Na and Cl.

Nutrient Salts and Agriculture.—Since the plant thus continues to absorb nutrient salts from the soil, this must become poorer in the particular substances unless the loss is repaired in some way. In nature this results from the fallen and dead parts of plants returning to the soil, and the salts contained in them becoming available for further life. In agricultural practice, however, a large proportion of the vegetation is removed in the crop, and the salts it contains are thus lost to the ground; at the most a fraction may be returned to the soil in the dung of grazing animals. The effect of manure in increasing growth, which has for ages been known to practical men, depends, at least in part, on the salts contained in it. Since, however, the amount of salts thus returned to the soil is insufficient to meet the loss, artificial manuring is required in agricultural practice ([10]). The first place among manures must be given to those which contain nitrogen, potassium, and phosphoric acid. Nitrogenous substances which are used, besides guano (which also contains phosphoric acid), are Chili saltpetre, ammonium sulphate, calcium cyanamide, and calcium nitrate; the two last have recently been artificially prepared from atmospheric nitrogen. Potassium is present in the Stassfurt waste salts, of which kainite is the most important since it also contains $MgSO_4$. As an important source of phosphorus, the so-called Thomas slag may be mentioned; this substance is formed in working ores containing phosphorus, and consists of triple phosphate of calcium. It can only be utilised by plants when in a state of very fine subdivision, as what is known as "Thomas-meal." Superphosphate is obtained by the treatment of calcium phosphate with sulphuric acid.

The Soil and Plant Geography.—From what has been said it might be concluded that a soil capable of supporting one kind of plant must be able to support any other species. Plant geography ([11]), however, shows that the composition of the soil exerts a great influence on the distribution of plants. This depends, on the one hand, on the fact that different plants make different demands on the amount and solubility of the essential food-materials, and on the degree of acidity of the soil; on the other hand upon the presence in the soil of substances other than the indispensable salts. The influence of these non-essential substances is different upon different species of plants. For example, $CaCo_3$ has a poisonous effect on some plants, and NaCl upon others, while other plants can endure large doses of these substances.

The effect of the soil upon the distribution of plants does not depend merely upon its chemical nature. The physical properties of soils (see p. 223) play an important rôle. Further, a plant may be absent from a locality, which, so far as the nature of the soil is concerned, would be suitable, because its seeds have never been brought to the spot.

III. The Absorption and the Movement of the Nutrient Salts in the Green Plant

All the chemical changes which take place in the metabolism of the plant are carried out in WATERY SOLUTIONS. For this reason WATER IS AN INDISPENSABLE CONSTITUENT of the plant. All actively living portions of the plant are permeated with water. The cell-walls contain imbibed water, in the cell-lumen are the large vacuoles filled with watery sap and the protoplasm, the basis of life, always contains 75 per cent or upwards of water. The plant can only carry on its life fully when in this condition of saturation with water. Any considerable diminution in the amount of water either destroys the life permanently, or at least so greatly diminishes the manifestations of life that they can no longer be observed.

It is evident that when a plant grows it must absorb water. But the amount of water utilised in growth is slight compared with the amount given off to the atmosphere from the aerial parts of the plant, especially the leaves. The loss of water in transpiration must be made good by absorption from the soil by the roots and conduction of the water to the leaves. The importance of this stream of water continually passing through the plant lies in the fact that the necessary nutrient salts are dissolved in it and are thus carried to all the places where they are needed.

The problem may be divided into three parts (12): (1) the absorption of the water and the nutrient salts dissolved in it; (2) the giving off of water in transpiration; (3) the conduction of the water.

1. The Absorption of Water and Nutrient Salts

(a) The Absorption of Water.—If, for the sake of simplicity, the absorption of pure water by the plant is first considered, an accurate analysis of the process shows that two physico-chemical phenomena are involved, viz., osmosis and imbibition.

Without a knowledge of the laws governing these phenomena the whole problem would be incomprehensible and they will therefore be first considered.

Osmosis (13).—If two solutions of unequal concentration, or a solution of some substance and the solvent, are separated by a partition which is permeable to both, a process of diffusion will commence. Such diffusion taking place through a partition or membrane is termed OSMOSIS. If a U-tube divided by such a PERMEABLE membrane (Fig. 229, 1) is filled on the one side with pure water and on the other with a solution of copper sulphate, the molecules of $CuSo_4$ will pass through the membrane and mix with the pure water; molecules of water will also pass through the membrane into the solution of $CuSo_4$. Ultimately equilibrium will be established between the two arms of the tube when equal quantities of water and of $CuSo_4$ are present on the two sides of the partition. If the partition is more easily penetrated by one of the two substances, this will pass more rapidly than the other, but in this case also an equal concentration of the solution on the two sides will in time result. The case is different, however, when the partition is SEMI-PERMEABLE, *i.e.* if it is only permeable for the molecules of water, while the molecules of $CuSo_4$ are unable to pass through it. The result will be a greater accumulation of water on the side of the partition where the $CuSo_4$ is (Fig. 229, 2).

The determining factor for the movement of the substance is thus the nature of the membrane.

Such semi-permeable membranes play an important part in the absorption of water by the plant. In studying the phenomena and laws of osmosis consideration of the natural vegetable-cell may be deferred, and an artificial cell with a semi-permeable membrane and containing an osmotically active substance be considered in the first instance. Semi-permeable membranes are obtained if a solution of copper sulphate comes in contact with a solution of potassium ferrocyanide, or a solution of gelatine with one of tannic acid. In order to give the membrane the requisite support it is deposited on a porous wall of baked clay. The clay-cells employed in galvanic elements coated on the inside with copper ferrocyanide are satisfactory for the purpose. The cell is filled with a solution of cane-sugar or of common salt and fitted with a mercurial manometer as shown in Fig. 230.

If such an osmometer, as this artificial cell is called, is immersed in a solution of the same concentration (*i.e.*, which has the same number of molecules to the litre, the same molecular number) nothing will happen. The system is in equilibrium.

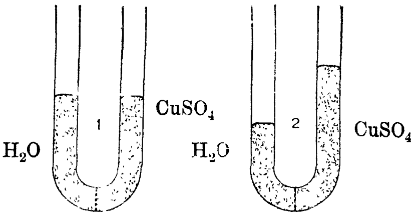
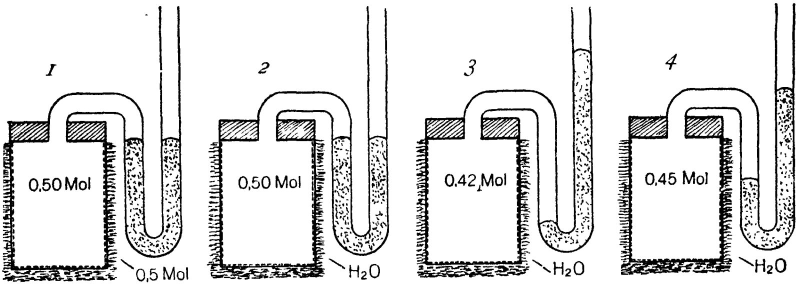


FIG. 229.—1. Permeable membrane. 2. Semi-permeable membrane.

It is otherwise if the cell is placed in water or in a solution of less concentration. What then occurs is illustrated by Fig. 230, 2, 3, 4, which show the beginning, the end, and an intermediate stage in the process. The concentration of the water within the cell is evidently less than that in the surrounding liquid, since in the concentrated solution of copper sulphate a large proportion of the molecules of water is replaced by molecules of $CuSo_4$. As a result the water, in correspondence with its higher concentration, will endeavour to pass into the osmometer. This may also be expressed by saying that the cell has a capacity of attraction for water, it exerts a SUCTION-FORCE. This is large to begin with but will become smaller and smaller; since, as the water enters, the concentration of water-molecules in the cell becomes greater, and that of the $CuSo_4$-molecules less, *i.e.* the solution becomes more dilute. But there is another reason for the suction-force diminishing. The entering water increases the volume of liquid in the osmometer and raises the level of the mercury in the manometer. This exerts a hydrostatic pressure on the inner wall of the cell which is naturally opposed to the suction-force. This pressure may be termed "wall-pressure" or "osmotic pressure," and its amount can be determined by the rise of mercury in the manometer. At the beginning of the experiment this pressure on the wall is evidently zero, it rises with the entrance of the water till at the final stage it has attained its maximum. At this stage the pressure is so great that no further entrance of water is possible. THE OSMOTIC PRESSURE THUS ALWAYS ACTS AGAINST THE SUCTION-FORCE. The greater the former becomes the less is the latter. It follows from what has been said above, that for every solution of a definite concentration the suction-force for water can be determined if, on placing the osmometer in water, the manometer is filled with the amount of mercury required to just prevent any water from entering the cell. Investigation shows that the suction-force is then equal to the osmotic pressure which the enclosed solution can develop. Every solution of a definite concentration has thus a value for the maximum suction-force it can exert. This value is called the "suction-force value of the cell-contents" or more shortly the "osmotic value" of the fluid.

It is necessary to distinguish between the maximum osmotic value (suction-force value) of the cell-contents and the actual osmotic value of the cell. The former is, according to our deductions, the maximal suction-force that the particular cell-contents is capable of. The actual suction-force of a cell may be much less than this. In order to obtain it the wall-pressure must be subtracted from the osmotic value (suction-force value) of the cell-contents, according to the equation.



Vol.	=100	Vol.	=100	Vol.	=120	Vol.	=110
Conc.	=0·5 Mol.	Conc.	=0·5 Mol.	Conc.	=0·42 Mol.	Conc.	=0·45 Mol.
Osmot. Pr.	=0·0 Atm.	Osmot. Pr.	=0·0 Atm.	Osmot. Pr.	=11·7 Atm.	Osmot. Pr.	=5·9 Atm.
Suction-force	=0·0 Atm.	Suction-force	=14·3 Atm.	Suction-force	=0·0 Atm.	Suction-force	=6·8 Atm.

FIG. 230.—Osmotic conditions in an experiment with the osmometer. (After URSPRUNG.)

Suction-force of cell = suction-force of cell-contents − wall-pressure.*

Since the concentration of a cell when it is submerged in water always becomes less owing to the absorption of water, the suction-force value of the cell-contents will always fall (Fig. 230, 2-4). From what has been said it is further evident that the volume of the cell-contents must alter; it is least at the beginning of the experiment when the cell is placed in water and becomes greater the more of this

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[NOTE. The significance attached to these terms is different in English works on physiology. In them "osmotic pressure" is usually equivalent to what is here termed "suction-force of cell-contents" and is thus distinct from the "wall-pressure." Cf. STILES, *Permeability*, pp. 98, 99.]

is absorbed. In order to make the study of these complicated relations clear, a definite example (0·5 mol.) was taken in the experiment shown in Fig. 230; from this the variations of the values under consideration here can be ascertained. The connections which subsist between them are graphically represented in Fig. 231.

In the experiment so far considered we have started with a definite concentration (0·5 mol.). When the osmometer is filled with solutions of different concentrations it is found that, within certain limits, the maximal possible osmotic pressure is proportional to the concentration of the solution. Thus PFEFFER found the following maximal values for various percentage solutions of sugar in the osmometer.

Sugar (percentage by weight).	Pressure (in cms.)	Max. osmotic pressure (in atmospheres).
1	53·8	0·71
2	101·6	1·34
4	208·2	2·74
6	307·5	4.04

If other organic substances, that do not undergo dissociation, are compared with cane-sugar it is found that generally the osmotic effect is proportional to the number of molecules in the solution: EQUIMOLECULAR SOLUTIONS ARE ISOTONIC (ISOSMOTIC). On this account it is more convenient to use molecular normal solutions instead of percentage solutions. In solutions of compounds that undergo dissociation, *e.g.* salts, the separate ions act osmotically along with the undissociated molecules. A solution of 0·1 mol. KNO_3 has therefore a much greater osmotic action than 0·1 mol. cane-sugar. The number which expresses by how much the osmotic value of a solution is greater than an equimolecular solution of sugar is termed the ISOTONIC COEFFICIENT of the solution.

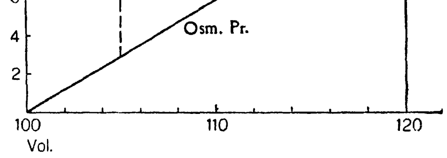

FIG. 231.—Graphic representation of the osmotic conditions in the experiment shown in Fig. 230. S_z = Suction-force value of the cell.

The experiments made with the clay-cell can be applied to the vegetable-cell. In the plant-cell represented in Fig. 233 the cell-wall corresponds to the clay cell itself, and the protoplasmic layer to the precipitation membrane of copper ferrocyanide. The protoplasm, so long as it is alive, is almost semi-permeable (14), while the cell-wall (like the clay-cell) is permeable. The cell-sap enclosed within the protoplasmic utricle corresponds to the solution filling the artificial cell. When a plant-cell is placed in water, it, like the clay-cell, will take up water; its volume increases; an osmotic pressure (wall-pressure) arises which presses the protoplasmic layer against the cell-wall and distends the latter. As in the artificial cell the increasing pressure of the column of mercury renders the absorption of water more and more difficult, so in the living cell a corresponding counter-pressure is produced by the distension of the elastic cell-wall; ultimately, when this has become equal to the osmotic force of the cell-contents, any further entrance of water is rendered impossible. The cell is now saturated with water.

The distension of the cell-wall is often considerable and depends on the amount of the internal pressure and the elastic properties of the cell-wall. In many cases the cell-wall is stretched by the pressure some 10 to 20 per cent, in extreme cases even 50 per cent, and it contracts when the pressure ceases. When the cell is pricked or the protoplasm killed, the pressure is removed and the wall contracts (Fig. 232). By the distension the cell-wall becomes more rigid, just as a thin india-rubber balloon when air is forced into it resists changes of shape. A cell the wall of which is stretched by the internal pressure is termed TURGESCENT; the internal pressure is spoken of as TURGOR (15).

The increase of rigidity of the plant, by reason of the turgor-pressure or turgescence, is very important; it is the simplest, and in many cases the only way, in which the cell becomes rigid. This is dependent naturally upon the presence of a sufficient supply of water; if a distended cell is taken from the water and allowed to give up water in the air, the stretching of the wall disappears, and with this the rigidity; the cell wilts. With a fresh supply of water the turgescent condition can be restored.

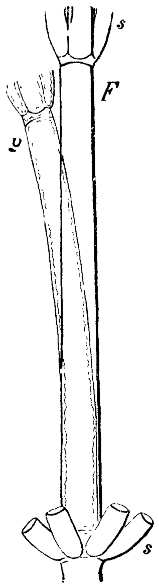

FIG. 232.—Internodal cell of *Nitella*. *F*, Fresh and turgescent; *p*, with turgor reduced, flaccid, shorter and narrower, the protoplasm separated from the cell-walls in folds; *ss*, lateral segments. (× circa 6. After NOLL.)

Since a manometer cannot be fixed to the vegetable cell, the direct measurement of its osmotic pressure is impossible. This can, however, be done indirectly by the study of the phenomena of PLASMOLYSIS. If a turgescent cell is placed in a solution of cane-sugar which has a higher osmotic value than the cell-sap (and is therefore termed hypertonic) the first change is a shortening of the cell, which goes on until the stretching of the wall has been completely lost. After this follows a withdrawal of the protoplasmic layer from the cell-wall, since the latter can itself contract no further; the protoplasmic layer continues to follow the vacuole as it diminishes in volume. The separation of the protoplasm from the cell-wall (plasmolysis) commences at the angles and leads ultimately to a rounding-off of the completely separated utricle, (Fig. 233). It is immaterial what substance is used to bring about plasmolysis so long as it does not injure the protoplasm, and that the latter is impermeable to it. In many ways cane-sugar is the most suitable; potassium nitrate, which was formerly extensively employed in such experiments, belongs to a class of substances to which the protoplasm is more or less permeable.

When by systematic trials the concentration of the plasmolysing solution has been ascertained which just effects the first separation of the protoplasm at the angles of the cell, it is possible to say that this plasmolytic limiting concentration has the same osmotic value as the cell-sap of the cell which has just lost its turgescence. If, for example, it has been found that the limiting concentration is 0·2 mol. cane-sugar, the cell-sap is isosmotic (isotonic) with 0·2 mol. cane-sugar; the sugar-value of the cell-sap amounts to 0·2 mol. Since the osmotic value of various concentrations of cane-sugar has been determined by the osmometer and by other physical methods (^{15a}) it is known how great the osmotic pressure of the plant-cell is when it is placed in water. If the cell-wall is much thickened, and therefore almost inextensible, the cell-sap cannot be diluted by entering water; such a cell, when saturated with water, can attain the maximal value physically possible. When the wall is extensible, a dilution of the sap always occurs with the increase of volume, just as in the case of the artificial cell. If we assume that a plasmolysed cell can increase its volume at saturation twofold, the concentration of the sap, and therefore its maximal osmotic pressure, will fall to one-half of what would have been the value had no increase of volume been possible. Only by carefully taking account of the alterations in volume of the cell during plasmolysis, can conclusions be safely drawn as to the actual osmotic pressure in a cell from its sugar value. In most cases the osmotic value is determined with KNO_3 instead of sugar. For ordinary cells the potassium nitrate

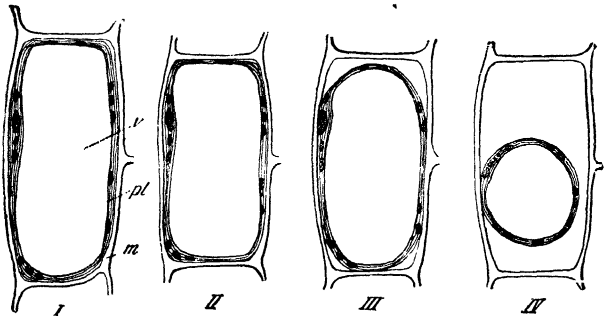

FIG. 233.—A young cell from the cortical parenchyma of the flower-stalk of *Cephalaria leucantha* (Compositae). *m*, Cell-wall; *pl*, protoplasm; *v*, vacuole. *I*, In water; *II*, in 4 per cent potassium nitrate solution; *III*, in 6 per cent solution; *IV*, in 10 per cent solution. (After DE VRIES.)

value is 0·15 to 0·30 mol.; it can, however, rise to 3 or more mol. Further, it tends to differ in adjacent cells by 0·1-0·2 mol., and to show periodic alterations owing to external conditions ([16]).

The separation of the protoplast from the cell-wall does not take place so smoothly as shown in Fig. 233. The protoplasm tends to remain connected to the wall by fine strands which rupture later.

On transference to pure water the turgescent condition will be regained, if the protoplasm has not been injured by the solution. If the protoplasm is killed, however, it has become completely permeable, and the necessary condition for a one-sided pressure has disappeared. Fresh living slices of the Beetroot when placed in pure water do not allow the colouring matter to escape from the uninjured cells. If the protoplasm is killed, the pigment passes into the surrounding water.

The potassium nitrate value is specifically different for different cells. High osmotic pressures are found, *e.g.*, in nodes of grasses (0·5-1·0 mol.), and certain desert-plants (3·0 mol.). The highest pressures are met with in plants which, like those of the sea and seashore, live in solutions of common salt, or, like some fungi, succeed in concentrated sugar solutions. In these cases the osmotic pressure of the cell always exceeds that of the surrounding solution; it is adapted and capable of regulation in relation to the medium, and is therefore not always the same ([17]). It is easy to understand why cells with such high osmotic pressures burst when transferred to less concentrated solutions or to pure water.

There are wide differences also in the potassium nitrate value between the different organs of a plant. Thus it was found by BLUM for *Fagus* that the epidermis of the lower side of the leaf had a potassium nitrate value of 0·365; the spongy parenchyma of 0·571; the palisade parenchyma of 1·017; the tissue of the outer cortex of the stem of 0·671; the cambium of 0·634; and the medullary-ray cells of the wood of 0·938 mol.

Imbibition ([18]).—There is another method by which many vegetable cells take up water. When, for instance, a dry seed is placed in water, its total volume and weight increase as a result of the swelling of its cell-walls and cell-contents. This increase in volume which such a body undergoes, owing to the introduction of water into it, is termed IMBIBITION. The water penetrates into the smallest portions of the material, *e.g.* the cell-wall. If after imbibition this is again allowed to dry, no air-filled cavities are found where the water was; the material has contracted. There are differences in the behaviour of different bodies capable of imbibition. Some, in which the swelling is limited, for example a piece of glue in cold water, can only take up a definite, limited amount of water; others in which the swelling is unlimited, for instance gum arabic, continue to absorb water till they pass into colloidal solution. The cell-wall belongs to the former class; it soon reaches its maximum swelling due to imbibition when it is placed in water. In this process the absorption of water is at first very active, it slows down more and more as the penetration of the water continues. The amount of water taken up differs for different materials. Thus the walls of lignified cells absorb $\frac{2}{3}$ of their weight, while the walls of some Algae and of some seed-coats and pericarps absorb several times their weight of water. In contrast to the cell-walls the protoplasm may be placed in the second class of substances. The air-dry protoplasm of many seeds and spores imbibes water and swells, just as does the cell-wall. Like gum arabic, however, it loses the characters of a solid body and passes into a colloidal solution. This is the condition of the protoplasm, as a rule, in the actively living cell, though certain portions may have a firmer consistence. Colloidal solutions have, indeed, always the tendency to pass from the fluid (sol) condition to the gel condition.

The laws underlying the process of imbibition are in many ways similar to those which have been recognised above for osmosis Thus we can speak of an imbibition-pressure and of the suction-force of a swollen body. By imbibition-pressure is understood the mechanical pressure that would have to be applied to a swelling body to just prevent further imbibition and increase of volume. In the early stages of swelling this pressure is at its greatest, but diminishes considerably as imbibition proceeds. In correspondence with this, the suction-force of a body at the beginning of the swelling process is extraordinarily high; much higher than the osmotic pressure exerted by a concentrated solution. It diminishes, with the absorption of water and associated increase of volume, to values similar to those met with in osmosis. In the living cell such bodies as the protoplasm and cell-wall are found in such a state that the forces due to imbibition are in equilibrium with those produced by the osmotically active substances. The pressure exerted on the cell-wall by the two suction-forces acting together is the turgor-pressure. A change in one of the two suction-forces always leads to a corresponding change in the other ([19]).

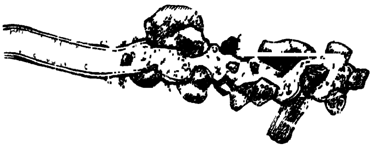
FIG. 234 —Tip of a root-hair with adhering particles of soil. (× circa 240. After NOLL.)

The Absorption of Water by Multicellular Plants.—In many lower plants all the living cells take part in the absorption of water. In more complex plants only the superficial cells are in contact with the supply of water in the environment, and absorption of water is limited to them. In higher plants the absorption of water is limited to the epidermal cells of the roots. The sub-aerial parts of the plant, covered with a more or less strongly-developed cuticle, cannot, under natural conditions, absorb sufficient water for the needs of the plant. The root, on the other hand, is highly specialised for this purpose, both as regards its external form and the structure of its limiting layer. Since the water in ordinary soils is finely subdivided and held firmly by the particles of the soil, a large surface must be exposed by the absorbing root. This is attained by the extensive branching of the root-system and by the presence of root-hairs which become attached to the finest particles of the soil (Fig. 234).

The plant is connected to the soil by the numerous lateral roots and their root-hairs, and can thus obtain the water held by capillarity in the soil, as soon as by loss of water a power of suction has arisen in the root-hairs. A plant can extract water even from a soil which appears dry. As absorption from such a soil continues the plant begins to wilt, but even in this state absorption is still taking place, though it does not go so far as to obtain the last traces of water from the soil. The osmotic forces are greater than the forces of capillarity and adhesion by which the particles of soil hold water. The process continues further in desert-plants according to FITTING, since their cell-sap is highly concentrated and can develop a very strong osmotic suction (20).

BRIGGS and SHANTZ have determined the water-content of the soil at the moment of wilting. This they term the COEFFICIENT OF WILTING and express it as a percentage of the dry weight of the soil. They find that it has nearly the same value in different plants, but differs widely in different soils. Thus the coefficient of wilting in coarse sand is 0·9, in fine sand 2·6 to 3·6, in sandy loam 9·9, and in clayey loam up to 16·5.

The Influence of the Nature of the Soil on the Water Absorption of the Plant (21). In most cases the soil obtains its water from atmospheric precipitation. Part of the rain-water percolates into the subsoil and the rest is retained by the soil. In the latter case the water is absorbed by the particles of soil and also held by capillarity in the cavities between the particles; since however, some of the particles are capable of swelling, it is partly held as water of imbibition The amount of water that can be retained by a soil shows wide differences that depend mainly on the size of the particles of the particular soil. According to the sizes of the particles the following types of soils are distinguished :

	Size of Particles.
Coarse Gravel-Rock	> 20 mm.
Fine Gravel	20–2 mm.
Coarse Sand	2–0·2 mm.
Fine Sand	0·2–0·02 mm.
Coarse Clay	0·02–0·002 mm.
Fine Clay or Colloidal Clay	0·002 mm.

The water-capacity, *i.e.* the maximum amount of water retained, of a clay soil is large, little water percolating through it; on the other hand it is small for a sandy soil through which water percolates readily. When the drainage of the percolating water is mechanically prevented, the water will gradually fill all the cavities in the soil and displace the air. The result is a swampy soil which, on account of its deficiency in oxygen, is very unfavourable for the development of most plants.

Besides the water precipitated as rain, the water in the subsoil plays a part in the water-content of a soil, especially in rainless periods, since it can be drawn up by capillarity. Soils with small cavities are naturally more effective in this respect than those in which the cavities are larger. There is an associated danger, however, for fine-grained soils continue to raise the deeper water to the surface; with continued evaporation the soil is dried to a considerable depth. In a sandy soil, on the other hand, only the water in the uppermost layers of the soil can be evaporated. Thus, in the latter case the water present in the deeper portions remains available for the use of plants. Fine grained soils, as a rule, undergo extreme variations in their water-content. It follows from what has been said that the physical properties of the soil have an important bearing on the geographical distribution of plants.

Other Types of Absorption of Water.—Some plants do not obtain their water from the soil. They belong chiefly to two distinct ecological groups, the EPIPHYTES and the WATER-PLANTS. The morphological and anatomical peculiarities found in relation to the absorption of rain and dew by the sub-aerial organs have already been dealt with on p. 173 f.

(b) The Absorption of Nutrient Salts.—The nutrient salts can only be absorbed by the superficial cells of the plant when in solution. The question has to be considered in what way the dissolved substances reach the vacuole through the cell-wall and the protoplasm. It was seen in connection with plasmolysis (p. 218) that the protoplasm is more or less semi-permeable, *i.e.* permeable to water but only with difficulty to dissolved substances. If the protoplasm were really quite impermeable to the salts that have been considered above, not even traces of them could enter the cell-cavity. Practically, however, the impermeability of the protoplasm is perhaps not absolute for any substance; there are all grades, from substances that pass through the protoplasm as easily as water, to those that are almost incapable of passing through it. Substances that diffuse fairly quickly cause a transient plasmolysis. Alcohol, ether, and chloral hydrate diffuse with special rapidity and cause no plasmolysis. The permeability of the protoplasm is not always the same, and may be regulated according to the external conditions (22). The salts of alkalies, for example, determine an increasing impermeability as regards themselves, and the salts of the alkaline earths can also diminish permeability for the alkaline salts.

The absorption or not of a substance is determined not by the whole protoplasm but by its external limiting layer. In the further passage of the substance, from the protoplasm into the cell-sap, the wall of the vacuole exercises a similar power of selection. The cause of the SELECTIVE POWER, by reason of which different cells can appropriate quite distinct constituents or substances in different amounts from the same soil, is to be sought in this most important property of the limiting layers of the protoplasm.

From the same soil one plant will take up chiefly silica, another lime, a third common salt. The action of Seaweeds in this respect is especially instructive; living in a medium containing some 3 per cent of common salt and poor in potassium salts, their cells, nevertheless, absorb relatively little common salt, but accumulate potassium salts.

Every substance to which the limiting layers of the protoplasm are permeable must ultimately reach the same concentration in the vacuole as in the solution outside the cell when its absorption would cease. Practically it often enters in much greater amount than this. Thus, for example, only a trace of iodine is present in sea-water, but may be accumulated in such quantities in seaweeds for these to become a source from which it is commercially obtained. The cell has not only a selective power, but is also able to store up materials by converting them into insoluble or indiffusible forms.

Certain organic pigments ([23]) such as methylene blue are especially suited to demonstrate the entrance and accumulation. Many cells contain tannins in their vacuoles, and these substances form with the entering pigment a compound which is indiffusible or quite insoluble. For this reason the vacuole becomes deeply coloured or has blue precipitates, though the solution of methylene blue employed is extremely dilute. It is noteworthy that the protoplasm itself remains unstained and is not in any way injured, the pigment would be accumulated in dead protoplasm.

The accurate study of the passage of colouring matters through the protoplasm has afforded valuable information regarding the causes of permeability, without as yet leading to a generally accepted theory. It may first be remarked that all cells do not behave alike. Thus the cells adjoining the vessels absorb acid dyes readily while usually permitting the basic dyes to pass. Since only basic dyes are soluble in lipoids, *i.e.* in fats and fatty bodies (lecithin, cholesterin) and the acid dyes are insoluble, the view has been advanced ([24]) that the limiting layer of the protoplasm may consist of lipoids; with various modifications this view has many adherents. But this "lipoid-theory", like the other hypotheses to be mentioned, is open to serious objections. RUHLAND has developed in place of it the ultra-filtration theory ([25]), according to which the penetration of pigments depends on the size of their particles, the protoplasm acting like a sieve. According to TRAUBE'S theory ([26]) the power of a substance to lower the surface tension of water determines its absorption by a cell. Lastly, according to the views of HANSTEEN ([27]), the outermost layer of the protoplasm consists of phosphatides, which can in various ways be more loosely or closely placed under the influence of particular substances and external factors; in this way the permeability will be altered.

Under natural conditions some plants absorb the nutrient salts from water as do the plants in a water-culture experiment. This is the case in many water-plants in which the whole external surface is of use in absorption. Since the salts only exist in very dilute solution in the water, the need of an extended surface for this purpose is readily understood; this in part explains the frequent occurrence of finely divided leaves in water-plants. The salts dissolved in the water are not, however, sufficient for all aquatic plants; many absorb substances from the soil underlying the water by means of their roots, and do not succeed when deprived of roots.

As a rule in land-plants the salts are absorbed from the soil. The salts contained in the nutrient solution described above, or similar compounds, are constantly present in the water of the soil; some of them, however, in such small amount as only to suffice for the growth of plants for a short period. Other sources of supply of the food-salts must exist when such growth continues. In fact, the amount of salts dissolved in the soil-water is no measure of the fertility of the soil. The soil always contains food-salts, partly in an absorbed condition, and partly in mineral form which the plant has to render accessible.

This is effected mainly by the excretion of carbonic acid from the root-hairs. Many substances are much more readily soluble in water containing carbonic acid than in pure water.

The solution of solid rock by the plant may most readily be shown by allowing the roots to grow against smooth polished slabs of marble; the course of the roots is indicated by the etching of the surface.

There are other cases in which stronger acids than carbonic acid excreted by the plant are concerned in bringing minerals into a soluble form. This can hardly be doubted when felspar and mica are dissolved by certain Lichens (28). Fungi and Bacteria also frequently produce and excrete solvents of this kind during their metabolism, and may have a similar effect on insoluble substances in the soil.

Some soils, especially those containing much clay, lime, or humus, have the property of retaining potassium and ammonium salts, and in less degree salts of calcium and magnesium; these substances are not easily washed out of the soil but can be obtained by plants. This is spoken of as the power of absorption of the soil for the substances in question. This does not hold for all salts; thus, for instance, sulphates and nitrates are not absorbed.

When the substratum contains, in addition to water and nutrient salts, dissolved organic substances, these may be absorbed in the same way. Water-cultures show, however, that at least the typical green plant is not dependent on such substances. It is otherwise with the Fungi and other plants which resemble them in metabolism (p. 257).

In addition to water and nutrient salts, dissolved gases may also be absorbed by the roots. As a rule only oxygen need be considered. The main source from which gases are absorbed is the atmosphere.

2. The Giving off of Water

The water absorbed by the roots is conducted throughout the body of the plant and given off from the subaerial parts in the form of vapour or less commonly as drops of liquid water. The former process is known as TRANSPIRATION, the latter as EXUDATION.

Transpiration (29)

The vegetable cell, like every free surface of water or substance swollen with water (*e.g.* gelatine, mucilage), must give up water to the air so long as the latter is not completely saturated. Under certain conditions the loss of water from some parts of plants (*e.g.* roots, submerged portions, shade-plants) is very great. Such objects exposed to dry air, especially in the sun, lose so much water that they become collapsed, limp, and wilted, and ultimately dried up. The leaves borne on ordinary land-plants behave otherwise. At first sight no loss of water is perceptible from them; but they also wilt during a drought, which renders absorption of water from the soil difficult. If the supply of water to them is interrupted completely, as by cutting them off, the wilting occurs more speedily. If the cut branches are placed in water this is absorbed by the cut surfaces and wilting does not take place. That they as a rule do not wilt when in position on the plant evidently depends on the fact that water is supplied from below in equal amount to that evaporated from above. The giving off of water can be demonstrated by simple methods.

Transpiration can be very strikingly demonstrated by the change in colour of cobalt paper; filter-paper soaked in a solution of cobalt-chloride has when completely dried a blue colour which changes to red on the presence of water. If a small piece of this cobalt paper is laid on a leaf and protected from the dampness of the atmosphere by a slip of glass, the change in colour to red, that commences at once, indicates the transpiration; conclusions as to the quantity of water given off may be drawn from the greater or less rapidity of the commencement and progress of the change in colour. Exact information on this point can only be obtained by weighing experiments. The flower-pot must be so covered that no evaporation can take place from it. The loss of water-vapour by a plant is usually so great, as to be recorded on a common balance without great difficulty in the course of a quarter of an hour. No general statement can be made as to the amount of transpiration from a unit area of transpiring surface, for this depends on many external factors, *e.g.* temperature, light, supply of water, etc., as well as on the structure of the plant.

The process of transpiration takes place in this way. An epidermal cell exposed to the air will lose some of the imbibition water of its cell-wall by evaporation; this would go on until the cell-wall was dried by the air if a reserve of water were not obtainable from within the cell. This is in fact obtained from the protoplasm, from which the cell-wall, no longer fully saturated, withdraws imbibition water, and the protoplasm in turn makes good its loss from the vacuole. The movement of the water affects the interior of the cell, and brings about a concentration of the cell-sap. Thus the conditions are established for the cell to absorb water from an adjoining cell which is not itself transpiring, and the loss of water is thus conducted from the superficial cells where evaporation is taking place into the depths of the tissue. The amount of transpiration primarily depends on the permeability to water of the cell-wall. If the cell-wall is an ordinary cellulose membrane the amount of transpiration will be large; when the wall is covered with wax or cuticle, or impregnated with cuticular substance, it gives off little water. Comparative investigations on suitable objects, by means of cobalt paper, show how the transpiration diminishes with the increase in thickness of the cuticular layers until it ultimately becomes practically non-existent. Corky walls behave in the same way as cuticularised layers. In their outer covering of cork, cuticle, and wax, plants possess a protection from a too rapid loss of water. An apple or a pumpkin, fruits with well developed cuticles, or a potato tuber protected by a layer of cork from loss of water, will remain turgescent for a long time. The green organs of plants, on the other hand, which must be able to get rid of the surplus water in order to secure the concentration of the nutrient salts and to reduce their temperature, make little use of such protective coverings. On the contrary, it has been seen (p. 158) that they are provided, besides the adaptations to regulate the transpiration, with special contrivances for promoting evaporation. Their great surface extension may be specially mentioned.

Transpiration is not, however, limited to the cells which are directly in contact with the atmosphere; an enormous number of internal cells can get rid of water-vapour when they abut on intercellular spaces. The air-filled intercellular spaces would clearly, after a short time, become completely saturated with water-vapour were they completely closed. Communications exist, however, as we have seen, between the atmosphere and the intercellular spaces, the most important being the stomata (p. 48). The aqueous vapour can escape by these, and thus the condition of saturation of the air in the intercellular spaces is not complete. The water-vapour escaping from the stomata is readily recognised by means of cobalt paper. If pieces of this are laid at the same time on the upper and lower surfaces of a leaf that has stomata only on the lower side, a change of colour will quickly take place in the cobalt paper on this side, while the blue colour will persist for a long time in the paper on the upper side.

It is usual to distinguish stomatal and cuticular transpiration, and we may thus say that only the stomatal transpiration is of importance in the typical land plant. In plants inhabiting damp localities the cuticular transpiration becomes considerable. Though the openings of the stomata are extremely small (cf. p. 49) they are usually present in enormous numbers and very suitably distributed. When it is taken into consideration that, as NOLL has shown, a medium-sized Cabbage leaf is provided with about eleven million, and a Sunflower leaf with about thirteen million stomata, it is possible to estimate how greatly evaporation must be promoted by diffusion through these innumerable, minute but closely placed perforations in the cuticular membrane, which itself allows practically no water to pass.

The smallness of the pores is indeed advantageous for transpiration. BROWN and ESCOMBE have shown that by diminishing the size of the pores in an evaporating surface while at the same time a corresponding increase in number of the stomata takes place, the total loss of water in transpiration is increased.

A further important property is that stomata not merely facilitate transpiration, but can stop it; they serve to REGULATE the transpiration, which a cuticle cannot do. The width of the pore of the stoma can be altered by changes in the guard-cells. When the pore is fully opened transpiration is maximal, and when it is completely closed transpiration sinks to zero. Since the opening and closing of the pore take place in accordance with the needs of the plant, the stomata are organs which react in a wonderfully purposive fashion. Opening is caused by illumination and by a certain degree of humidity of the air; on the other hand, darkness or dry air effect a closing of the pore.

The movements of the guard-cells are movements of irritability and are brought about by changes in turgescence. As a consequence of the peculiar thickening of the elastic cell-walls of the guard-cells (p. 50), an increase of the turgor-pressure intensifies the curvature of the cells and a diminution of turgor lessens the curvature. The former change leads to the opening of the pore and the latter to its being closed, as will be evident from Fig. 235 without further description (cf. also Figs. 45-47).

An increase of turgor could result from more water being available for the osmotically active contents of the guard-cells to attract. As a matter of fact it comes about from a considerable increase in the osmotic value of the guard-cells under the conditions of increased illumination and humidity. The osmotic value on the other hand diminishes with shading and dryness.

This increase in the osmotic value of the sap of the guard-cells is to be mainly related to the solution of the starch deposited in the chromatophores, *i.e.* its conversion into an osmotically active substance. Correspondingly the fall in osmotic value is brought about by the re-forming of this starch. The enzyme on which the solution of the starch-grains depends is rendered active by a number of different stimuli, some of chemical and others of physical nature; similarly the regeneration of the starch can be determined in various ways. The influence of light on the enzymatic process in the guard-cells is especially important. According to the investigations of LINSBAUER and STALFELT, a sudden change in the strength of the illumination is recognisable within 3-5 minutes by an alteration in the size of the stomatal pores (30).

The stomata are mainly present on the leaves, which are thus to be regarded as organs of transpiration (and of assimilation, p. 240). The amount of water evaporated from the leaf-surfaces is surprising (31). For instance, a strong Sunflower plant, of about the height of a man, evaporates, in a bright day, over a litre of water. It has been estimated that an acre of Cabbage plants will give off two million litres of water in four months, and an acre of Hops three to four millions. For a Birch tree with about 200,000 leaves and standing perfectly free, VON HÖHNEL estimated that 300-400 litres of water would be lost by evaporation on a hot dry day; on an average the amount would be 60-70 litres. A hectare of Beech wood gives off on the average about 20,000 litres daily. It has been calculated that during the period of vegetation the Beech requires 75 litres and the Pine only 7 litres for every 100 grammes of leaf substance. For every gramme of dry, solid matter produced, 250-900 grammes of water are evaporated on the average.

It is evident from these and similar experiments that more water is evaporated in a given time from some plants than from others. These variations are due to differences in the area of the evaporating surfaces and to structural peculiarities (the number and size of the stomata, presence of a cuticle, cork, or hairy covering, etc.). But, even in the same shoot, transpiration is not always uniform. This is attributable to the fact that, both from internal and external causes, not only the size of the openings of the stomata varies, but also that transpiration, just as evaporation from a surface of water, is dependent upon external conditions. Heat, as well as the dryness and motion of the air, increases transpiration for purely physical reasons; while light, for physiological reasons, also promotes it. From both physical and physiological causes, tranpiration is more vigorous during the day than night. Plants like *Impatiens parviflora*, which droop on warm days, become fresh again at the first approach of night.

In order to arrive at a proportional measurement for the physiologically active forces and the evaporation due to the atmosphere, the transpiration of the leaf may be compared with the evaporation from an equal surface of pure water under the same external conditions. The ratio, transpiration : evaporation (T/E) which is always less than 1, may be termed relative transpiration. This conception must, however, be employed with caution, because, with an alteration in the external factors, the evaporation from a free water-surface follows other laws than the giving off of water-vapour through a multiperforate membrane (32)

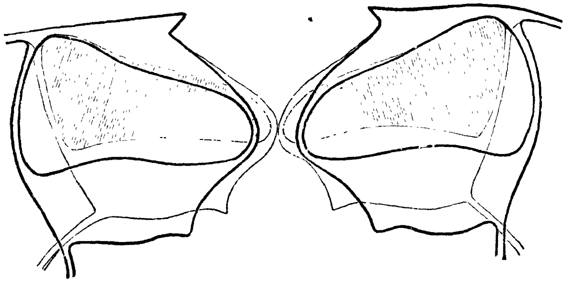

FIG. 235.—Stoma of *Helleborus sp.* in transverse section. The darker lines show the shape assumed by the guard-cells when the stoma is open, the lighter lines when the stoma is closed. (After SCHWENDENER.) The cavities of the guard-cells with the stoma closed are shaded, and are distinctly smaller than when the stoma is open.

Information as to the condition of opening (33) of the stomata can be obtained by the use of cobalt paper (cf. p. 227) or by the method of infiltration. If the stomata are open, fluids such as petroleum, alcohol, etc., easily penetrate and inject the whole system of intercellular spaces; the leaf thus becomes translucent. If a strip of black paper is laid across a leaf the underlying stomata close. On treatment with alcohol the appearance represented in Fig. 236 is then obtained. The open condition of the stomata may also be demonstrated by the method of gaseous diffusion. If a red leaf containing anthocyanin with its stomata open is placed in air containing ammonia, a blue colour develops in a few seconds; this does not take place if the stomata are closed. More recently the porometer devised by F. DARWIN for the measurement of the width of the stomatal openings has been employed. It consists of a small glass bell (Fig. 237 G) which is closely cemented to the leaf (B). The enclosed air, by means of a suction applied at Q, is brought somewhat below atmospheric pressure; the pressure is measured by the water-manometer (T). The rapidity with which the pressure in the bell and the atmospheric pressure are equalised gives a measure of the condition of opening of the stomata.

Plants of dry habitats which require to economise the absorbed water show numerous arrangements which protect them against excessive transpiration (cf. p. 159). In plants living in very damp situations, on the other hand, arrangements to further transpiration are found. When the leaf is able, either by absorption of heat from without or by the production of heat within itself (p. 273), to raise its temperature above that of its surroundings, transpiration is still possible even in an atmosphere saturated with aqueous vapour. In the process of exudation the plant has a further means of giving off water even after transpiration has completely stopped.

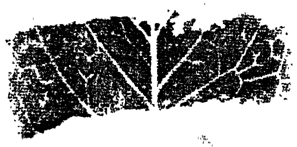

FIG. 236.—A leaf of Lilac darkened in the middle while the ends were exposed to light. Only the illuminated stomata remain open and allow the absolute alcohol to enter. (After MOLISCH.)

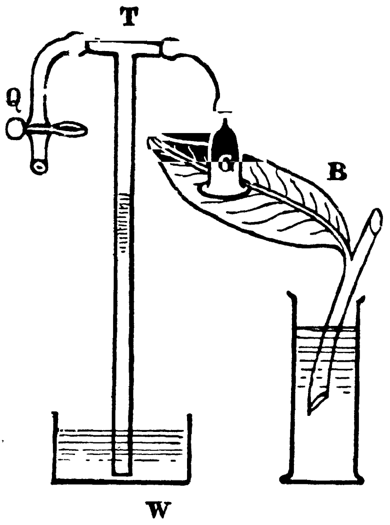

FIG. 237.—Porometer after F. Darwin. B, leaf; G, glass chamber; T, manometer; Q, compression clip; W, water.

Exudation (34)

The discharge of water in a liquid state by direct exudation is not of so frequent occurrence as its loss by transpiration, but is found under special conditions, viz. when the plant is saturated with water and the air is saturated with water vapour. Early in the morning, after a warm, damp, but rainless night, drops of water may be observed on the tips and margins of the leaves of many of the plants of a meadow or garden. The drops gradually increase in size until they finally fall off and are again replaced by smaller drops. These are not dewdrops, although they are often mistaken for them; on the contrary, these drops of water exude from the leaves themselves. The drops disappear as the sun becomes higher and the air warmer and relatively drier, but can be induced artificially if a glass bell-jar be placed over the plant, or the evaporation in any way diminished. The excretion of drops from the leaves can be brought about by artificially forcing water into cut shoots.

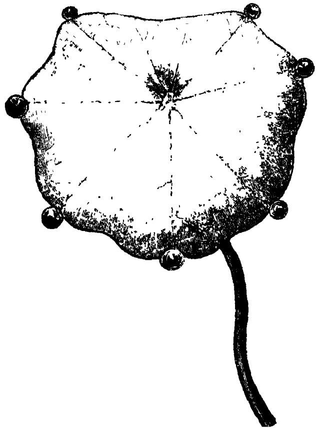

FIG. 238.—Exudation of drops of water from a leaf of *Tropaeolum majus*. (After NOLL.)

The drops appear at the tips of the leaves in Grasses, on the leaf-teeth of *Alchemilla*, and from the blunt projections of the leaves in *Tropaeolum* (Fig. 238). They come from so-called WATER-STOMATA (p. 110) or through ordinary stomata, or they are secreted by small pits or hairs (sometimes by stinging hairs). All such water-excreting organs are termed HYDATHODES.

The excretion of liquid water is far more common in moist tropical forests than in temperate climates. Such exudations of water are particularly apparent on many Aroids, and drops of water may often be seen to fall, within short intervals, from the tips of the large leaves. From the leaves of *Colocasia nymphaeifolia* the exuded drops of water are even discharged a short distance, and 190 drops may fall in a minute from a single leaf, while $\frac{1}{10}$ litre may be secreted in the course of a night. Again, in unicellular plants, especially some Moulds, the copious exudation of water is very evident, the water in this case is pressed directly through the cell-walls.

Since the excretion of water in the liquid form can occur when the conditions are unfavourable to transpiration, especially in submerged water-plants, it may in a sense take the place of transpiration in maintaining the current from the water-absorbing organs. Its physiological significance is not, however, the same as transpiration, since the expressed water always contains salts, and sometimes also organic substances in solution. In fact, the quantity of salts in water thus exuded is often so considerable that after evaporation a slight incrustation is formed on the leaves (the lime-scales on the leaves of Saxifrages and the masses of salt in some halophytes, p. 213). In some instances, also, the substances in solution in the water may play the main physiological part in the process as in the case of the secretions of the NECTARIES, of the DIGESTIVE GLANDS of insectivorous plants (p. 262), and of some STIGMAS.

Bleeding.—Exudation of water may often be observed after a plant has been wounded; it is regularly seen in trees and shrubs when cut in the spring, and is especially well marked in the Vine. In shrubs cut off a short distance above the ground, the extrusion of water from the wound is readily demonstrated. In this weeping or bleeding of wounds the water comes from the vessels and tracheides, and is pressed out with considerable force (ROOT-PRESSURE).

If a long glass tube be placed on the root-stump and tightly fastened by rubber tubing, the exuded fluid will be forced up the glass tube to a considerable height. How great the force of this pressure is may be shown by attaching to the stump a manometer (Fig. 239). The column of mercury will in some cases be forced to a height of 50 or 60, and under favourable conditions to 140 cm. or more (in the Birch). These pressures would be sufficient to raise a column of water 6, 8, and 18 metres high.

The amount of water extruded is especially great when the soil is kept moist and warm ; it continues under such conditions, according to the kind of plant and its stage of development, some days or even months. The water may amount to many litres: up to 1 litre per day in the Vine, 5 litres in the Birch, and 10-15 litres in Palms. In parts of plants that continue bleeding for some time a certain periodicity in the amount is noticeable ; more is extruded by night than by day.

The outflowing sap often contains, in addition to mineral salts, considerable quantities of organic substances (dissolved albuminous matter, asparagin, acids, and especially carbohydrates). The amount of saccharine matter in the sap of some plants is so great that sugar may be profitably derived from it. The sap of the North American sugar-maple, for example, contains ½ per cent of sugar, and a single tree will yield 2-3 kilos each spring. The sap of certain plants is also fermented and used as an intoxicating drink (birch wine, palm wine, pulque, a Mexican beverage made from the sap of *Agave*, etc.). One inflorescence of *Agave* will yield 1000 litres of sap in from four to five months.

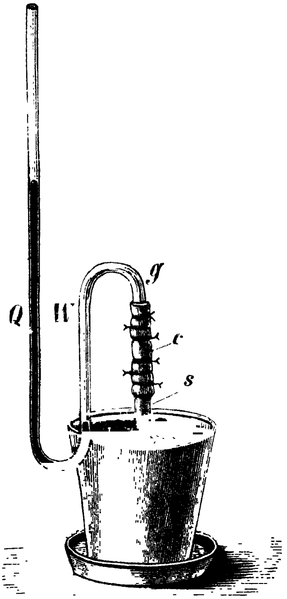

FIG. 239.—Vigorous exudation of water as the result of root-pressure from a cut stem of *Dahlia*. The smoothly-cut stem *s* is joined to the glass tube *g* by means of the rubber tubing *c*. The water *W*, absorbed by the roots from the soil, is pumped out of the vessels of the stem with a force sufficient to overcome the resistance of the column of mercury *Q*. (After NOLL.)

Causes of the Excretion of Water (^{35}).—The excretion of drops of water from intact plants is in part due to an active excretion of water from superficial cells. In other cases water is forced into the vessels, and finds a way out at the points of least resistance (p. 110). In the phenomenon of bleeding, also, water is forced from parenchymatous cells into the cavities of the vessels; although this process takes place especially often in roots, it is not always absent in the cases of stems and leaves.

Thus, when fully analysed, all the phenomena described show a one-sided excretion of fluid from living cells. The causes of such glandular activity of the cells cannot be entered into here.

3. Conduction of Water (36)

The water which is given off from the leaves has been absorbed by the roots. It has thus to traverse a path which, even in annual plants, may amount to some metres, and in the giants of the vegetable kingdom may be more than 100 m.; the stems of *Eucalyptus amygdalina* are 100 m., those of *Sequoia gigantea* 95 m. in height. Osmotic passage from cell to cell would bring about the movement of this water far too slowly to cover the loss. The movement of water for this purpose, or, as it is called, the TRANSPIRATION STREAM, is practically confined to the woody portion of the vascular bundles, *e.g.* the wood of trees. This is shown by the classical experiment of ringing a woody stem. Over a short extent of a branch all the tissues external to the slender column of wood are removed. Since the leaves of this branch remain as fresh as those of the other branches it is evident that the transpiration current must pass through the wood and not through the cortical tissues. On the other hand, when a short length of the wood is removed from a stem without at the same time unduly destroying the continuity of the cortex, the leaves above the point of removal will droop as quickly as in a twig cut off from the stem. This experiment can be performed either on intact plants or on cut-off branches placed in water; the latter for a time, until changes have taken place at the cut surface, absorb water as actively as does the intact plant by its roots. When a branch is cut off and the cut surface is placed in a solution of gelatine, which penetrates for some distance into the vessels and can then be allowed to solidify, the wood will be found to have lost its power of conducting water. This shows that the cavities of the vessels are essential for water-conduction.

In water-plants and succulents, in which little or no transpiration takes place, the xylem is correspondingly feebly developed. On the other hand, the transpiring leaf-blades have an extraordinarily rich supply of vascular bundles; these anastomose freely, so that any particular point is sure to obtain sufficient water. The conducting tracts in the stem leading to the leaves form, especially in trees which grow in thickness, a wonderfully effective conducting system. All the wood of a thickened stem does not serve this purpose; water-conduction is limited to the more recently developed annual rings. When a heart-wood (p. 149) is formed this takes absolutely no part in the process.

As regards the forces which maintain this stream of water it has already been seen (p. 222) that the water is absorbed by means of the suction-force of the epidermis of the root and especially of the root-hairs. From the epidermis it has to be conducted across the inner layers of cells of the root to the vessels. In these it ascends until it reaches the leaves. Here again, there are several layers of parenchymatous cells to be traversed before the water reaches the cells that actually give it off. The movement of water in the plant is diagrammatically represented in Fig. 240. There are evidently three questions to be answered: 1, how does the water reach the vessels; 2, how is it conducted in the vessels, and 3, how does it reach the peripheral cells of the leaves from the vessels?

The water can only be conducted from the epidermis of the root if the suction-force increases on passing inwards across the cortical cell-layers. On the other hand the suction-force of the cells in the leaf must increase on passing outwards. URSPRUNG and BLUM have made measurements which show that in the case of the root the suction-force of the cortical cells does actually become greater and greater until the endodermis is reached. In the leaves it was shown in a corresponding fashion that the cells of the spongy parenchyma have a greater suction-force than the parenchymatous cells abutting on the vessels, and the value for the palisade cells is still greater. These results may be illustrated by an example.

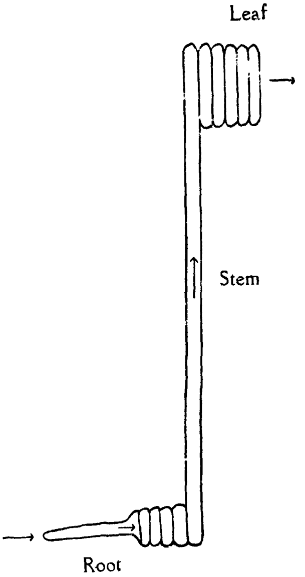

FIG. 240.—Diagrammatic representation of the movement of water in the plant. (After WALTER.)

The cells of the roots of *Phaseolus*, 1 cm. behind the tip, showed in a particular case the following values for their suction-force, expressed in atmospheres (36):

Epidermis.	Cortex: Layer 1	2	3	4	5	6	7
0·3	0·5	1·5	1·8	2·0	1·8	2·2	2·3

Endodermis.	Pericycle.	Wood-parenchyma.
1·6	1·4	1·6

The leaf of *Hedera helix* gave the following values:

Upper Epidermis.	Palisade-parenchyma.	Spongy parenchyma.	Lower Epidermis.
8·3	13·0	10·2	7·8

The suction-forces show ascending values from the epidermis to the endodermis of the root. The cells of the endodermis, and those of the pericycle and the parenchyma cells around the vessels further in, show a diminished value. There is a sudden alteration at the endodermis. In order to explain continued water-conduction by means of the suction-forces through these and the more internal cells, **Ursprung** has resort to a hypothesis of a non-homogeneous suction-force. It is assumed that each of the cells of the endodermis has a higher suction-force on the side towards the epidermis, and that this is greater than the suction-force of the adjoining innermost cortical cell; on the other side of the endodermal cell, that turned inwards towards the vessels, the suction-force is much less.

Thus when in the above example the value of 1·6 atmospheres was determined for the endodermis this would be an average between (say) 2·5 atmospheres for the suction-force to the outside and 0·7 atmosphere for the suction-force to the inner side. If the cells further in behave in the same way, a stream of water from the epidermis to the vessels could come about in spite of the fall in osmotic value apparent at the endodermis.

In the second example the parenchymatous cells that surround the bundle are not included. **Ursprung** has however shown that their suction-force value is similar to that of the epidermal cells. If the epidermal cells have constantly a lower value than the cells of the palisade and spongy parenchyma it is clear that they are not supplied with water from the latter; they will take water directly from the larger veins where the sheaths of the latter abut on the epidermis.

Turning to the question as to how the water moves in the vessels there is still uncertainty as to the forces which give rise to the transpiration stream. It is natural to think of a pressure acting from below, or a suction from above, and to regard the former as due to root-pressure, the latter to the process of transpiration. There are, however, a number of reasons against ascribing the movement of the water to root-pressure. The other possibility, that it is mainly the suction-force arising from transpiration which raises the considerable amount of water to the summit of high trees, has at present many adherents; but there are still many gaps in the proof of this COHESION THEORY.

The following points have to be considered as regards the root-pressure. In many plants the root-pressure actually observed is very slight or absent. Even in plants with a powerful root-pressure the amount of water thus supplied in a given time is considerably less than that lost in transpiration. With somewhat more active transpiration, therefore, the root-pressure is not manifested in the way described above. When an actively transpiring plant is cut across above the root, no water is at first forced from the stock; but, on the other hand, if water is supplied to it the cut surface absorbs it greedily (there is evidence of a negative pressure). Only after it is fully saturated does the forcing-out of water commence. In nature root-pressure thus only comes into play when transpiration is greatly lessened, for instance at night when the air is damp and cool. The most favourable conditions for this phenomenon occur in spring when, on the one hand, the wood is richest in water, and, on the other, the transpiring foliage is not fully developed. On wounding the xylem the sap then oozes in drops out of the vessels and tracheides. A positive root-pressure in trees with foliage appears only to occur in tropical forests.

Many facts in support of the cohesion theory have been adduced. A cut shoot placed with its lower end in water shows by remaining fresh that it is able to raise the water to its uppermost twigs. This does not fully exhibit the amount of suction-force which the shoot can exert, for if the latter is connected with a long tube filled with water it can support a water column of 2 metres or more in height. If the end of the tube is dipped into mercury even this heavy fluid will be lifted to a considerable height. Strong and otherwise uninjured branches of Conifers are able to raise the mercury far above the height of the barometric column, without showing signs of wilting. Necessary conditions for such a suction are on the one hand an air-tight closing of the water-conducting tracts, and on the other hand a considerable cohesive power of the fluid to be raised. The cohesion of water has been found to attain a high value ; according to the measurements of URSPRUNG and RENNER it may reach at least 350 atmospheres. Thus it is possible to picture the pull exerted by transpiration being transmitted by the cohesion of the water to the tips of the roots. If the cohesion theory is correct it should be possible to demonstrate a considerable tensile force in the conducting tracts, and RENNER believes that proof of this is forthcoming (^{37}). The experiments of this investigator have weakened another objection to the theory and shown that the frictional resistance which the water experiences in its passage through the narrow vessels is not too great to be overcome by the suction-forces. Since the frictional resistance naturally increases with the length of the conducting tracts, and thus in the plant from above downwards, the demonstration by HUBER that a corresponding increase in the suction-forces in the leaves accompanies an increase in the resistance is important for the cohesion theory (^{38}). There is difficulty in demonstrating the continuous water-columns in the conducting tracts required by the theory. It has recently been shown by BODE that such continuous water-columns exist in transparent herbaceous stems, and that they are not broken even by the considerable increase of the tensile force that accompanies wilting (^{39}).

It is not out of the question that the living elements, always present in the vascular strands, may play a part in the raising of the water.

IV. The Nutrient Materials derived from the Atmosphere

While water and salts are, as has been seen, as a rule absorbed from the soil, the air contains substances which are necessary to the successful existence of the plant, and must be termed food-materials. These are carbon dioxide and oxygen. They are as a rule, obtained from the atmosphere. Only submerged water-plants obtain them from the water, in which case they are absorbed in the same way as other dissolved substances.

Oxygen.—When a plant is deprived of oxygen, all vital manifestations sooner or later cease (cf. p. 289). Since oxygen is also essential to the human organism, this fact does not seem surprising.

Carbon Dioxide.—It appears at first sight much less self-evident that carbon dioxide should be indispensable to the plant, and yet this is the case. While no source of carbon is offered to the plant in a water-culture, it grows in the food-solution, and accumulates carbon in the organic compounds of which it consists ; the only possible conclusion is that the plant has utilised the carbon dioxide of the atmosphere. Carbon dioxide is present in ordinary air in the proportion of 0·03 per cent ; thus a litre contains 0·3 ccm. If such air is passed over a green plant exposed to bright light, it can be shown that the carbon dioxide diminishes in amount or disappears. Colourless parts of the plant, or organisms like the fungi which are not green, behave differently; they absorb no carbon dioxide. If a green plant is placed in a bell-jar and supplied with air freed from carbon dioxide, its growth soon stops, and increase in dry weight ceases completely. Carbon dioxide is thus an indispensable food-material, and is evidently the source from which the plant obtains its carbon. The small proportion of this gas present in the atmosphere is quite sufficient for the nutrition of plants (p. 245). A supply of organic compounds of carbon in the soil or culture-solution does not enable a plant to dispense with the carbon dioxide of the air; in any case CO_2 is the best source of carbon for the green plant which we are at present considering. Neither is it sufficient to supply such a plant with carbonic acid in the soil or culture-solution; it requires to be supplied directly to the leaves.

Other Gases.—Oxygen and carbon dioxide are the only gases which are necessary to the ordinary green plant. For most plants the nitrogen of the atmosphere is of no use (cf. p. 259).

Absorption of Gases.—Carbon dioxide and oxygen in part enter the epidermal cells, and partly pass by way of the stomata into the intercellular spaces, from which they reach the more internal tissues.

There are no air-filled canals or spaces in the cell-wall or the protoplasm through which gases could diffuse into the cell. Thus absorption of gases is only possible in so far as they are soluble in the water permeating the protoplasm and wall. The gases behave like other dissolved substances and diffuse into the cell. They diffuse through cell-walls more easily the richer in water these are. The ordinary cell-wall, when in a dry condition, hardly allows gases to diffuse through it (40); in nature, however, the cell-wall is always more or less saturated with water. The cuticle, on the other hand, has very little power of imbibing water, and places considerable difficulty in the way of any osmotic passage of gases; it is not, however, completely impermeable.

The gaseous diffusion takes place rather through the water with which the cell-wall is impregnated than through the substance of the wall itself. Since carbon dioxide is much more readily soluble in water than is oxygen, it will be evident that it will pass more rapidly through a cell-wall saturated with water than oxygen will. In all probability this holds for the cuticle as well. Since, however, the partial pressure of the oxygen in the air is relatively considerable, while that of carbon dioxide is very slight, oxygen can pass in sufficient quantity through the cuticle, but carbon dioxide cannot; on this account we find that all organs which only require to absorb oxygen are unprovided with stomata, while organs which absorb carbon dioxide always have stomata.

In the soil as well as in the air, plants, as a rule, find so much oxygen that this gas is able to pass through the epidermis. Organs which live in swampy soil which is poor in oxygen form an exception to this. In marsh-plants, which stand partly in the air, the large intercellular spaces form connecting canals through which the atmospheric oxygen without being completely used up can reach the organs growing deep in the swampy soil and cut off from other supplies of oxygen. In some cases (especially in Palms and Mangroves) the need of a supply of oxygen to such roots is met by specialised roots (PNEUMATOPHORES) which project vertically from the muddy soil (Fig. 181), and absorb oxygen from the air.

The efficiency of the stomata in gaseous exchange varies with the width to which the pores are open. The closure of the pores of the stomata, which may be brought about in maintaining a sufficient supply of water, not only arrests transpiration, but also prevents the entrance of CO_2 into the plant.

It has been seen in considering the giving off of water-vapour that the stomata, in spite of their small size, facilitate diffusion on account of their enormous numbers and their distribution. This also applies to the absorption of carbon dioxide. Thus, for example, a square metre of the leaf-surface of *Catalpa* absorbs about two-thirds the amount of carbonic acid gas taken up in an equal time by the same area of 3-10% soda solution freely exposed to the air.

The Movement of Gases from cell to cell and their interchange between the cells and the intercellular spaces takes place by diffusion. In the intercellular spaces, movements in mass due to pressure are also concerned. Unequal pressure is set up by the warming or cooling of the air in the intercellular spaces, or by movement of the part of the plant leading to changes of shape. The intercellular spaces form a highly-branched system of cavities communicating with one another and with the atmosphere. The communication with the outside is effected in the first instance by the stomata, and also by the lenticels and organs of similar function (pp. 48, 56); both diffusion and movements in mass of the gases go on through these openings.

That the intercellular spaces were in direct communication with each other and also with the outer atmosphere was rendered highly probable from anatomical investigation, and has been positively demonstrated by physiological experiment. It is, in fact, possible to show that air forced by moderate pressure into the intercellular passages makes its escape through the stomata and lenticels; and conversely, air which could enter only through the stomata and lenticels can be drawn out of the intercellular passages. The porometer described on p. 230 demonstrates clearly the connection between the intercellular spaces and the stomata.

Intercellular air-spaces are extensively developed in water- and marsh-plants (cf. p. 157), and may form two-thirds of their volume. The submerged portions of water-plants unprovided with stomata thus secure a special internal atmosphere of their own, with which their cells maintain an active interchange of gases. This internal atmosphere is in turn replenished by slow diffusion with the gases of the surrounding medium. As regards the rest of their gaseous interchange, these plants are wholly dependent on processes of diffusion, since stomata, etc. are wanting. Plants which possess these organs may also obtain gases by osmosis if the cuticle of their epidermis is permeable to gases.

V. The Assimilation of the Food-Materials in the Green Plant

The plant grows and continues to form new organs; for these purposes it continually requires fresh supplies of food-materials. The materials of the food become changed after their absorption, and the substance of the plant is built up from them. They are said to have been ASSIMILATED. By assimilation is understood the transformation of a food-material into the substance of the plant. Those processes of assimilation in which profound changes take place, *e.g.* the change from inorganic to organic compounds, are especially interesting. This is particularly the case when we are still unable to experimentally bring about the reaction outside the organism. The assimilation of carbon by the green plant is a process of this kind; in it organic carbon compounds originate from carbon dioxide.

A. ASSIMILATION OF CARBON DIOXIDE IN GREEN PLANTS (41)

The dry-weight of a green plant is increased when this is grown in a water-culture; half of this dry weight consists of carbon and this is not supplied in the culture-solution. The green plant obtains it from the carbon dioxide of the atmosphere and transforms this by the help of sunlight into sugar. In this process water takes part and oxygen is given off as is expressed in a summary fashion by the formula:

$$6CO_2 + 6H_2O = C_6H_{12}O_6 + 6O_2.$$

If we assume that the carbonic acid gas of the atmosphere (carbon dioxide, CO_2) becomes on its solution in the cell H_2CO_3, the formation of sugar would take place in two stages. In the first, oxygen would be given off and formaldehyde formed:

$$H_2CO_3 = HCHO + O_2.$$

In the second stage the aldehyde is polymerised to sugar:

$$6HCHO = C_6H_{12}O_6.$$

Thus, for every volume of carbon dioxide which is used up, an equal volume of oxygen is formed; in other words the relation of the oxygen to the CO_2 absorbed is the so-called "assimilation quotient" $\frac{O_2}{CO_2} = 1$. It has been shown by eudiometric measurements that this is the case. The oxygen given off can, however, even when it is only detected qualitatively, be used as an indicator of the decomposition of the carbonic acid. Thus, when a plant is enclosed along with phosphorus in a space free from oxygen and exposed to light, the formation of oxygen is shown by the white fumes given off from the phosphorus. Another means of drawing conclusions as to the production of oxygen by a green plant is afforded by the movements of certain Bacteria which previously lay motionless in the water from which oxygen was absent (p. 329). The clearest demonstration of assimilation is obtained by using certain water-plants such as *Elodea* or *Potamogeton*. If cut shoots or leaves of these plants are submerged in water and exposed to light, a brisk continuous stream of bubbles comes from the cut surface. If the gas is collected in considerable quantity in a suitable apparatus, *e.g.* in a test-tube (Fig. 241), it can be shown to consist not of pure oxygen but of a mixture of gases rich in oxygen; a glowing splinter bursts into flame in the gas.

The appearance of the bubbles of oxygen is explained in this way. The carbon dioxide dissolved in the water enters the green cells of the plant by diffusion and is there decomposed. The oxygen given off is much less soluble than carbon dioxide and therefore appears in the gaseous form. It passes into the intercellular spaces, causing there an increase of the pressure, and this is the cause of the appearance of bubbles of gas at every wounded surface.

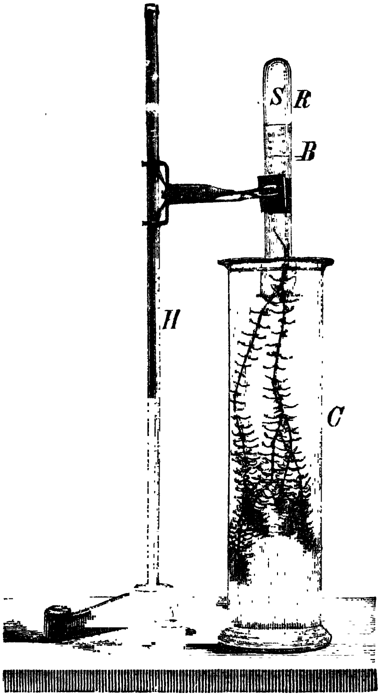

FIG. 241.—Evolution of oxygen from assimilating plants. In the glass cylinder *C*, filled with water, are placed shoots of *Elodea canadensis*; the freshly-cut ends of the shoots are introduced into the test-tube *R*, which is also full of water. The gas bubbles *B*, rising from the cut surfaces, collect at *S*. *H*, stand to support the test-tube. (After NOLL.)

The foundations of our knowledge of the assimilation of carbon dioxide by the green plant were laid, in the end of the eighteenth and beginning of the nineteenth centuries, by PRIESTLEY, INGEN-HOUSS, SENEBIER, and TH. DE SAUSSURE. The discovery is of extraordinary significance, for THE FORMATION OF ORGANIC MATERIAL FROM CARBON DIOXIDE BY THE GREEN PLANT IS THE PROCESS WHICH RENDERS POSSIBLE THE LIFE OF ALL OTHER ORGANISMS AND IN PARTICULAR OF ANIMALS UPON THE EARTH.

By means of the gas-bubble method it is easy to bring proof of the statement made above that only the green parts of plants, and these only in light, are able to assimilate CO_2. Thus the stream of bubbles from an *Elodea* which goes on briskly at a brightly-lit window becomes slower as the plant is brought into the middle of the room, and ultimately ceases when the intensity of the light is still such as to allow our eyes to read. Within certain limits assimilation increases in proportion to the intensity of the light. Similar experiments may be carried out using artificial sources of light. They show that all the methods of illumination in common use may be effective in the assimilation of CO_2. The rays of different wave-lengths are, however, by no means of equal use in assimilation ([42]).

In order to investigate the effect on assimilation of light of different wave-lengths, either the dissociation of light in the spectrum or light rendered monochromatic by colour screens may be employed.

On the whole the assimilatory effectiveness is limited to the visible rays in the neighbourhood of 0·4-0·8μ. Urspruna believes that he has demonstrated that both ultra-red and ultra-violet rays can also be utilised. The behaviour of the different rays has been much studied, but the results are still not clear. It is certain that the red rays of 0·68μ show the maximal absorption (Fig. 242) and also have a specially strong assimilatory effect. According to Engelmann there is a far-reaching correspondence between the absorption of light by chlorophyll and assimilation. Urspruna has investigated the starch-formation in light of all wave-lengths, arranged to afford equal light-energy. His results are represented in Fig. 243. This shows the parallelism with the absorption spectrum that might be anticipated ; it breaks down in the blue and violet region, because here, owing to the closure of the stomata, the supply of CO_2 is too small. Kniep and Minder, who have investigated the assimilation in light of different colours by the gas-bubble method, found that blue light is as effective as red when it provides the same energy.

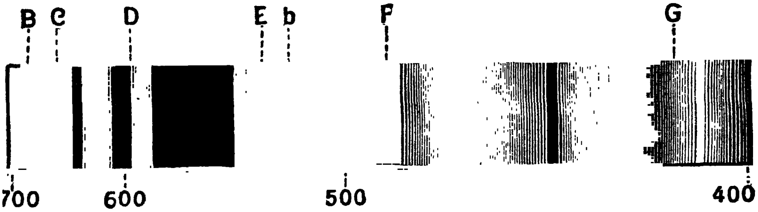

Fig. 242.—Absorption spectrum of chlorophyll according to Gr. Kraus. The Fraunhofer lines (B, C, etc.) are indicated above and the wave-lengths (700 μμ-400 μμ) below. The black and shaded regions are those where the light is absorbed or weakened.

Since sunlight is, in Nature, an indispensable factor in CO_2 assimilation it becomes at once clear why the foliage leaves have a flat expanded shape. Their large surface fits them to absorb the light. If their function of CO_2 assimilation is to be well performed the foliage leaves must not only have a large surface but also be thin. Willstätter's investigations showed that light which has passed through two foliage leaves is unable to exert any further assimilatory effect. The leaves must, however, contain a very large number of chlorophyll-grains. Their dark green colour shows that this is the case, and microscopical examination confirms this. Stems have far fewer chloroplasts than the leaves, and the roots and other subterranean organs have none at all.

Every investigation shows that organs without chlorophyll are quite unable to assimilate carbon dioxide. This holds not only for the organs of the plant but for the parts of the cell. The colourless protoplasm and the nucleus of the cell give off no oxygen when exposed to sunlight; this can readily be proved by the bacterial method. The chloroplasts alone are the active organs in CO_2 assimilation, and only when they contain chlorophyll; etiolated (p. 285) or chlorotic (p. 18) chloroplasts are not functional.

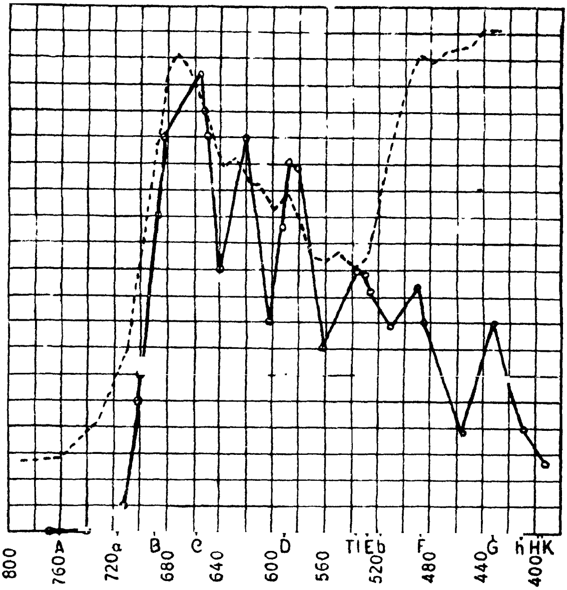

FIG. 243.—The unbroken line represents the dependence of starch-formation on the wave-length of light, when the light-energy supplied is equal for all the rays. The dotted line represents the radiation absorbed by the green pigment of living leaves, the entering radiation being represented by 100. On the abscissae the wave-lengths of light are given in $\mu\mu$ and some of the Fraunhofer lines are indicated. (Grating spectrum. After URSPRUNG.)

In the red-leaved varieties of green plants, such as the Purple Beech and Red Cabbage, chlorophyll is developed in the same manner as in the green parent-species, but it is hidden from view by a red colouring matter in the epidermis or in deeper-lying cells.

Only a relatively small percentage of the light which falls on the leaf and is absorbed is utilised in the assimilation of CO_2 (^{43}). That, however, light must disappear as such in CO_2 assimilation is clear, for from what other source than the energy of light could the energy be obtained that is stored up in the organic substance formed in assimilation? This potential energy of the organic substance of the plant serves to maintain the vital processes. The force exerted by our steam-engines is also to be traced to the assimilatory activity of the plants, the wood or the carbonised remains (coal, brown coal, peat) of which are burnt beneath its boiler. In the combustion of the reduced carbon compounds to carbon dioxide the energy, which was previously required to transform carbon dioxide into the combustible materials, again becomes free. There is thus in the formation of organic substance not merely a gain of indispensable constructive material, but also of energy in a form which allows of its ready utilisation in other parts of the plant (p. 269).

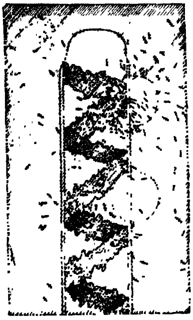

FIG. 244.—Cell of *Spirogyra* illuminated at the two circular areas. Accumulation of the bacteria only in the neighbourhood of the chloroplast. (× 250. After ENGELMANN.)

Since a supply of energy is required in CO_2 assimilation the formula given on p. 240 may be more completely given—

$$6\ CO_2 + 6H_2O + 674{,}000\ \text{cal.} = C_6H_{12}O_6 + 6O_2.$$

According to the investigations of BROWN and PURIEWITSCH it can be assumed that a leaf in Nature absorbs about 80 per cent of the total radiation falling on it, including both the invisible heat rays and the visible rays of light. By far the greater part of this goes to raising the temperature of the plant, for only 0.5-6.0 per cent is employed in assimilation. If, on the other hand, only the visible rays that are absorbed are taken into consideration the chlorophyll-apparatus is found to work very economically; WARBURG and NEGELEIN were able to show for the Alga *Chlorella* that at least 50 per cent of the absorbed visible rays of light were used in assimilation (44).

The assimilatory activity of a chloroplast, like every vital function, is dependent on a number of internal and external factors. To the internal factors belong the presence of the pigment chlorophyll and its situation in a living chloroplast. Chlorophyll itself, separated from the plant, is as little able to decompose the carbon dioxide as is a chloroplast which for any reason has not developed the characteristic pigment or has lost it (chromoplasts). Since, however, assimilation is not proportional to the amount of chlorophyll, it is necessary to assume with WILLSTÄTTER (45) that in addition to the pigment another factor is essential, whether this is the protoplasm of the chloroplast or an enzyme (p. 252) which it contains.

Among external factors sunlight as referred to above must be mentioned first, and next the presence of carbon dioxide. Since the latter is only present in small proportion in the air and its place cannot be taken by other compounds such as carbon monoxide, the life of plants, and with this the existence of all organisms, would ultimately cease were not fresh supplies of carbon dioxide continuously produced. The amount of carbon dioxide in the atmosphere is estimated at 2100 billion kilogrammes and the annual consumption by green land-plants at 50-80 billion kg.

It is thus clear that the supply would be used up in a few years by the vegetation (46) were it not continually renewed. This is in fact the case, for the continual construction of organic substance in assimilation is accompanied by a continual breaking down of such substances in respiration and combustion. The two processes must be on the whole equivalent; were it not so, it would be incomprehensible how organic life has existed for millions of years on the earth. At the present time there are always about 3 litres of CO_2 in every 10,000 litres of air; in winter the amount is somewhat greater (3.0-3·6 litres) and in summer somewhat less (2·7-2·9 litres). It is open to question whether these proportions have always held. It is not impossible that the percentage of carbon dioxide in the air may have been greater in earlier periods, and that the great development of the vegetation that resulted in the accumulations of coal may have stood in relation to this.

The following example will serve to illustrate the magnitude of the process. The average amount of CO_2 is about 3 litres in 10,000 litres of the atmosphere. This weighs about 7 grammes, of which $\frac{8}{11}$ is oxygen, and only $\frac{3}{11}$ carbon. Only 2 grammes of carbon are thus contained in the 10,000 litres of air. In order, therefore, for a single tree having a dry weight of 5000 kilos to acquire its 2,500,000 grammes of carbon, it must deprive 12 million cubic metres of air of their carbonic acid. From the consideration of these figures, it is not strange that the discovery of INGENHOUSS was unwillingly accepted, and afterwards rejected and forgotten. LIEBIG was the first in Germany to again call attention to this discovery, which to-day is accepted without question. The immensity of the numbers just cited is not so appalling when one considers that, in spite of the small percentage of carbonic acid in the atmosphere, the actual supply of this gas is estimated at about 2100 billion kilos, in which are held 560 billion kilos of carbon. The whole carbon-supply of the atmosphere is at the disposal of plants, since the CO_2 becomes uniformly distributed by constant diffusion.

These figures are also an indication of how great the converse processes of breaking down of carbonaceous compounds must be to maintain the supply of carbon dioxide at the same general level. By the respiration of the higher plants and animals, as well as by the combustion of coal, a considerable part of the organically combined C is again transformed into CO_2; the main part of the carbon dioxide is, however, probably returned to the air by bacteria living in the soil. Investigations have shown that the amount of the "soil-respiration" (*i.e.* the respiration of the micro-organisms living in the soil and of the roots of the plants), in the case of a field planted with wheat, would be sufficient to cover the requirements of CO_2 for the crop.

According to SCHRÖDER the carbon of 1100 billion kilogrammes of CO_2 is fixed in the land-plants of the world; about 90% of this is in the wood of trees. This amount is about one half of that contained in the atmosphere. Animals appear to contain much less carbon and only account for about 1% of the amount accumulated in plants.

Submerged water-plants absorb the CO_2 dissolved in water. Its amount varies considerably according to the temperature. At 15° C. a litre of water contains about as much CO_2 as a litre of atmospheric air. The dissolved bicarbonates which dissociate into carbonates and CO_2 also play an important part in the supply of carbon to aquatic plants. Artificially conducting carbonic acid through the water or the addition of bicarbonates increases, to a certain degree, the evolution of oxygen, and the assimilatory activity.

An increase in the proportion of CO_2 in the air, if it does not go too far, results in an increase in the assimilation. Thus by an artificial enrichment of the air in CO_2, a considerable increase of the agricultural crop would be obtained. There is no doubt that the beneficial effect of natural farm manure as compared with mineral manures is dependent in part on the continued active CO_2-production of the bacteria it contains; these find the requisite organic food-materials in the soil, and the CO_2 they produce in respiration is given off to the atmosphere (47).

The CO_2 assimilation, like all vital processes, is dependent on the temperature. It begins at a temperature a little above zero, reaches its maximum at about 37° C., and again stops at about 45° C.

These cardinal points not only have different positions in different plants but do not remain constant for any particular plant. This is especially true of the optimum, which in the course of a few hours may sink from 37° C. to 30° C. In bright warm weather assimilation does not reach its full possible value, since the supply of carbon dioxide is then insufficient.

Other less important factors need not be considered in detail. It may be mentioned, however, that many substances can bring about a temporary, or ultimately a permanent, limitation or arrest of the assimilatory process.

Till recently it was assumed, on the ground of BLACKMAN's work, that among the nnmerous factors which are simultaneously important in CO_2-assimilation, there was always one, viz., the one present in least amount, which determined the amount of assimilation (law of the minimum) Recent investigations (48) have, however, shown that sometimes an increase in the assimilation will result, both from increasing the intensity of the light and increasing the supply of carbon dioxide. Corresponding results have been obtained in the case of the nutrient salts, for which it was earlier held with LIEBIG that the law of the minimum held.

Products of the Assimilation of Carbon Dioxide.—It was assumed above that sugar was formed from the carbon dioxide, and analysis in fact shows that the amount of sugar in a foliage leaf is increased after exposure to sunlight. It is true that grape-sugar is neither always nor only shown to be present; usually other more complex carbohydrates appear. These can all, however, be traced back to hexoses like grape-sugar, and ultimately starch arises by the union of two or more molecules of hexose and the loss of the elements of water $[{}_nC_6H_{12}O_6 = (C_6H_{10}O_5)_n + {}_nH_2O]$. The occurrence of starch in the chloroplasts of illuminated foliage leaves is very common, but by no means general. When the leaves are placed in darkness for some time the starch disappears. When on the other hand a part of the plant from which the starch has been removed is exposed to sunlight, new starch grains (assimilation starch) often form in the chloroplasts in a surprisingly short time (5 minutes); these soon increase in size and ultimately exceed in amount the substance of the chloroplast itself.

Since starch is stained blue by iodine the commencement of assimilation can be readily demonstrated macroscopically (SACHS' method).

Leaves which have been in the light have their green colour removed by means of alcohol, and are treated with a solution of iodine; they take on a blue colour. If the amount of starch is greater the colour is a deeper blue or almost black. The depth of the coloration thus affords a certain amount of information as to the quantity of starch present. To demonstrate smaller amounts of starch the decolorised leaves are placed, before staining with iodine, in a solution of potash or of chloral hydrate in order to swell the starch-grains. This method of demonstrating assimilation can also be used to show that the starch only appears in the illuminated portions of the leaf If a stencil of opaque material from which, for instance, the word "Stärke" has been cut is laid on the leaf, the word "Stärke" will appear blue on a light ground, as in Fig. 245, when the leaf after being illuminated is treated with iodine. Instead of a stencil a suitable photographic negative can be used, as MOLISCH has shown; after illumination and subsequent treatment with iodine a positive photograph is obtained (Fig. 246).

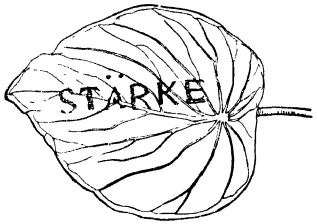

FIG. 245.—Assimilation experiment with the leaf of *Ariopsis peltata*. (Reduced.)

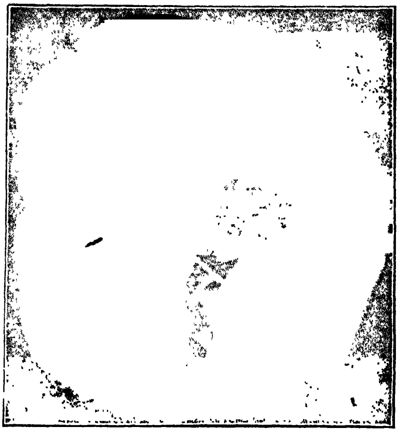

FIG. 246.—The positive photograph obtained by covering a leaf of *Tropaeolum* which has been freed of starch by the negative and exposing it to the sun. After assimilation the leaf has been treated with iodine. (After MOLISCH.)

In some plants (many Monocotyledons) no starch is formed in the chloroplasts, but the products of assimilation pass in a dissolved state directly into the cell-sap. Starch is formed, however, where there is a surplus of the products of assimilation. The guard-cells of the stomata and the cells of the root-cap of these Monocotyledons also contain starch. In other cases only a fraction of the product of assimilation appears as starch (in *Helianthus*, for example, only ⅛), while the rest remains as sugar or is otherwise made use of. It is thus clear that the amount of starch formed cannot always be taken as a measure of the assimilation.

Starch-formation can be induced to take place in the dark by floating leaves on a sugar solution of suitable concentration. This shows that the formation of starch does not stand in direct connection with the assimilation of carbon dioxide but is only the result of the accumulation of sugar in the cell.

In some algae neither sugar nor starch but other products of assimilation are formed, *e.g.* Floridean starch.

The Quantity of the Assimilated Material depends on the one hand upon the kind of plant and on the other upon the external conditions to which it has been exposed. It can be said that a square metre of leaf of an actively assimilating plant under optimal external conditions produces between 0·5 and 1 gramme of dry substance per hour. When it is considered how many square metres of leaf-surface are daily assimilating, a conception can be formed of the huge production of organic substance in this largest of all chemical factories. SCHRÖDER estimates the amount formed annually by land-plants as about 35 billion kg. The German harvest alone contained in 1912 some 9 milliards kilos of assimilated material in the cereals (rye, wheat, spelt, barley).

There are two methods (49) in use for determining the amount of assimilation. The method invented by SACHS is as follows. In the morning, portions of leaves, usually halves, are removed; their superficial area is measured and they are then dried and weighed. In the evening, equally large portions (the remaining halves) of the leaves which have been exposed to light throughout the day are similarly dried and weighed. The increase of weight indicates the gain to the plant by the assimilation of carbon. This is SACHS' half-leaf method. A quite distinct method of quantitatively determining the assimilation of CO_2 is that of KREUSLER. A leaf still attached to the plant is placed in a closed chamber through which a constant current of air passes; the amount of CO_2 removed from the air by the leaf is determined. The amount of sugar or starch which could be formed from this amount of CO_2 can then be easily calculated.

B. ASSIMILATION OF NITROGEN IN THE GREEN PLANT

Since a green plant obtains its carbon from carbon dioxide, which is only present in a very small proportion in the air, it might be assumed that the enormous supply of nitrogen in the air would form the primary and the best source of this element of plant-food. Every water-culture, however, shows clearly that atmospheric nitrogen cannot be utilised by the typical green plant. If combined nitrogen is omitted from the nutrient solution the plant will not grow.

In KNOP'S food-solution nitrogen was supplied as a nitrate, and this form is most suitable for the higher plants. Nitrites can also serve as a source of nitrogen, but in too high concentrations are injurious. Compounds of ammonia, *e.g.* ammonium sulphate, ammonium chloride, so long as they are not injurious to the plant owing to an alkaline reaction, *e.g.* ammonium carbonate, can also be utilised. Organic compounds of nitrogen also, such as amino-acids, acid amines, amines, etc., will serve for food, though none of them lead to such good results as are obtained with nitrates.

We are not nearly so well acquainted with the assimilation of nitric acid and of ammonia as we are with that of carbon dioxide. We do not know accurately the place in which the assimilation takes place, we know less of the contributory external conditions, and lastly, we are not clear as to the products of assimilation.

Ultimately, of course, albumin is formed, a far more complex substance than a carbohydrate, containing always, besides C, H, and O, some 15-19 per cent of N, besides S and in some cases P. The methodical study of the products of the breaking down of albumin gives some insight into the structure of the protein molecule. This shows that in albumin a large number of amino-acids are combined with loss of water. Since EMIL FISCHER has obtained albuminous substances (polypeptides) by a union of amino-acids followed by polymerisation, it is probable that in the plant also such amino-acids are first formed and then unite further. If the simplest amino-acid, glycocoll, $NH_2 \cdot CH_2 \cdot COOH$ (which, it is true, is not of wide occurrence in plants), is considered, it is evident that this can be derived from acetic acid $CH_3 \cdot COOH$ by replacing an atom of H with a NH_2 group (the amino group). Nitric acid, HNO_3, must therefore be reduced when its nitrogen is to be employed in the construction of protein. This reduction is independent both of sunlight and chlorophyll, so that nitric acid can be assimilated in darkness and in colourless parts of the plant (50). Indirectly, of course, chlorophyll and light are of importance in the synthesis of proteins in so far as compounds containing carbon are required, and these are formed in sunlight with the help of chlorophyll. On account of their rich supply of carbohydrates the foliage leaves are specially fitted for the production of protein, but they are not "organs of protein formation" in the same degree as they are organs for the formation of carbohydrates. While in many plants (nitrate plants, *e.g. Chenopodium, Amarantus, Urtica*) nitric acid can be recognised in the leaves, in most plants it appears to be transformed soon after its absorption by the root.

We know as little of the steps in the assimilation of ammonia as of those of nitric acid. Since no preliminary reduction is required, ammonia might be regarded as more readily assimilable than nitric acid. When ammonia is found to be less favourable in a water-culture than nitrates, this may be due to certain subsidiary harmful effects of the former substance.

The hypothetical intermediate products between the nitrogenous compounds absorbed and the completed proteids, *i.e.* various amino-acids and related substances, are present in all parts of the plant. Leucine, tyrosine, and asparagine are especially common. It can, however, rarely be determined whether these substances have been synthesised from ammonia or nitric acid or whether they have arisen by the breaking down of albumin (cf. p. 255) (51).

Nitrogen is present not only in proteins but in LECITHINS and in ORGANIC BASES. The former are complex esters in which glycerine is combined with two molecules of fatty acid, one molecule of phosphoric acid, and the nitrogen-containing base, choline. They are never absent from living protoplasm. The majority of organic bases (alkaloids) are probably by-products of the assimilation of nitrogen and are not further utilised.

C. ASSIMILATION OF OTHER SUBSTANCES IN GREEN PLANTS

Sulphuric acid most nearly resembles nitrogen since it also is used in the construction of proteins which contain about $\frac{1}{2}$–$1\frac{1}{2}$ per cent of S. It is still uncertain where and under what conditions its assimilation occurs; we only know that a reduction must take place in the process. In some plants sulphur is combined in other substances besides proteins.

Phosphoric acid is connected with sulphuric acid in so far as it is employed in the construction of at least some protein substances, (nucleo-albumin) and especially of the nucleo-protein of the cell nuclei; it forms from 0·3 to 3 per cent of this. In entering into the molecule of this substance the phosphoric acid, unlike sulphuric acid, is not reduced. Lecithin, which is present in all plants, also contains phosphorus, and this is also the case for phytin, which occurs especially in seeds.

The Metals.—As may be shown by the method of water-culture, potassium, calcium, magnesium, and iron are just as essential as any of the substances hitherto mentioned. It is very probable, at least for potassium and magnesium, that they take part in the construction of certain compounds that are essential for the existence of the plant. Possibly protoplasm contains these elements. Other substances also may contain them; thus, for instance, a considerable amount of magnesium has been shown to exist in chlorophyll. It was formerly believed that chlorophyll contained iron because the chloroplasts remained yellow when iron was omitted from the food-solution (chlorosis, p. 212). It is now known that chlorophyll does not contain iron and that iron is also necessary for plants that are not green. This supports the assumption that protoplasm itself contains iron, and that the chlorosis which occurs when iron is wanting is a result of a diseased condition of the protoplasm.

Since potassium, magnesium, and iron thus pass into the substance of the plant they must be assimilated, but we know nothing of how or where this happens. The case of calcium is somewhat different; it is not invariably essential, for some algae can succeed without it. In other plants it has a protective function, preventing the poisonous effects which result from iron, magnesium, potassium, and sodium, and also from phosphoric acid, sulphuric acid, nitric acid, and hydrochloric acid, perhaps owing to their action on the colloids of the plant. Oxalic acid, which exerts a poisonous action on the protoplasm, is produced in the construction of amino-acids; calcium neutralises this by transforming it into the insoluble and harmless calcium oxalate. It is, however, improbable that the indispensability of calcium in the case of the higher plants is merely due to this protective function.

Water.—We know that water is essential to the plant. When it is taken into the plant as water without undergoing chemical change we do not speak of its "assimilation." This is the case, for example, for the water which fills the vacuoles of cells or that which permeates the protoplasm and cell-wall. It is different where the water is chemically combined. This necessarily takes place when carbohydrates are formed from carbon dioxide, and probably in other cases also. In these cases there is the same justification for speaking of the assimilation of the water as of the assimilation of carbon dioxide.

VI. Translocation and Transformation of Assimilates in Green Plants

The assimilates serve primarily for the construction of new substance of the plant and the growth of new cells. They are also employed as reserve materials and as substances in course of translocation, while some are used up in the metabolism and others in the production of excretions and secretions.

It is only rarely, however, that growth takes place where the work of assimilation is effected. Thus the assimilation of carbon dioxide goes on mainly in fully-grown foliage leaves while the growing points are more or less distant from the leaves. The assimilatory activity and the formation of new organs also do not coincide in time. Many plants have periods of active assimilation when but little growth is taking place and, alternating with these, periods of active growth associated with little or no assimilatory activity. Our trees lose their leaves in autumn and herbaceous plants lose all the above-ground organs. In both cases new organs of assimilation must be formed in spring before assimilation can be resumed; in the growth of these organs the plant utilises stored assimilates. Every germinating seedling also lives at first wholly at the expense of assimilates of a preceding generation. Such stored-up assimilates, mainly carbohydrates, fats, and proteids, are termed RESERVE MATERIALS. They may be deposited where they are formed or may be carried to secondary places of deposit. Every foliage leaf which in the evening of a bright summer's day is gorged with starch is an illustration of the first condition. The second is seen in seeds where reserve materials are stored in the endosperm or the cotyledons. It is also found in vegetative organs, which may even show by their form that they are places for storage of reserve materials; examples of these are the swollen leaves of bulbs, swollen stems (*e.g.* potato), or swollen roots (*e.g.* turnip). In order that assimilates should reach these storage places they must be capable of TRANSLOCATION, and they have also to be conveyed through the plant when they are removed from the place of storage and employed in the development of new organs. Many reserve materials or assimilates occur in a solid form which does not allow them to pass from cell to cell; starch is an example of this. Others are, it is true, soluble, but have such large molecules that they only diffuse with difficulty. For these reasons reserve substances have usually to undergo a change before they can be conveyed through the plant.

A. MOBILISATION OF RESERVE MATERIALS

In the mobilisation of reserve materials we have usually a not very profound change of the nature of a hydrolysis, *i.e.* a splitting of the substance into smaller molecules with the absorption of water. This must be separately considered for the three main types of reserve material, the carbohydrates, the fats, and the albuminous substances.

1. Carbohydrates

Starch is one of the most important reserve materials in plants. It not infrequently forms the main part of the reserve substance in seeds as well as in tubers and bulbs. In the potato tuber 25 per cent and in the grain of wheat 75 per cent of the fresh weight consists of starch. It is also present in considerable amounts in the pith, the xylem-parenchyma, the medullary rays, and the rind of trees. Starch is completely insoluble and has to be broken down in order to allow of its translocation. This is effected technically by treatment with acids; the grape-sugar of commerce is obtained by treating potato-starch with sulphuric acid. The molecule of starch is split up into numerous molecules of dextrose according to the formula

$$(C_6H_{10}O_5)_n + nH_2O = nC_6H_{12}O_6.$$

In the plant this hydrolysis is effected not by means of acids but by a special substance called DIASTASE. Diastase can be extracted from the organs by water or glycerine, precipitated by means of alcohol from the extract and again dissolved, without any essential change in its properties. On the other hand, diastase is rendered inactive by heating.

Diastase has the same effect on starch as sulphuric acid has; it does not break down the starch as completely but stops after forming the disaccharide malt sugar (maltose). Diastase and sulphuric acid both act as catalysts. The name catalysts is given to substances which influence the rapidity of a chemical reaction. We are mainly concerned with the acceleration of reactions. The usual method in the chemical laboratory of accelerating a reaction is the application of heat; the fact that the life of the organism is confined to a narrow range of temperature limits this method. A second method is by the use of inorganic catalysts. Many of these, such as sulphuric acid mentioned above, injure the protoplasm; it is thus easy to understand why the organism should form special catalysts that are not injurious. These are termed ENZYMES (52) and occur in both plants and animals. While many inorganic catalysts influence very various chemical processes, the influence of organic catalysts is usually quite specific; thus diastase only acts on starch. Since the catalyst either does not enter into the reaction or at least does not do so permanently, a small amount of it is able to hydrolyse a large quantity of the substance acted on, if the products of the reaction are continually removed. The chemical nature of diastase and other enzymes is still doubtful (53).

Diastase is found in many parts of the plant, especially in those which contain much starch, such as foliage leaves and germinating seeds. The amount of diastase in an organ is not constant, but is regulated according to the needs of the plant; further, its action can be arrested by the formation of other enzymes (anti-enzymes). This is one of the many regulatory processes so characteristic of the organism.

In the plant diastase acts on the starch-grains. These are corroded under its influence; they are dissolved away from without inwards, but this proceeds as a rule irregularly, so that the shape of the grain changes. At particular spots the diastase eats more quickly into the grain and, using pre-existing splits and canals, breaks it up into smaller portions which then dissolve further (Fig. 247). Outside the plant the action of diastase can best be shown on thin starch-paste (cf. p. 33); on adding diastase to this the characteristic iodine reaction is lost after a few minutes or a quarter of an hour. The blue colour given at first, changes to a wine-red tint, and ultimately a yellow colour is given.

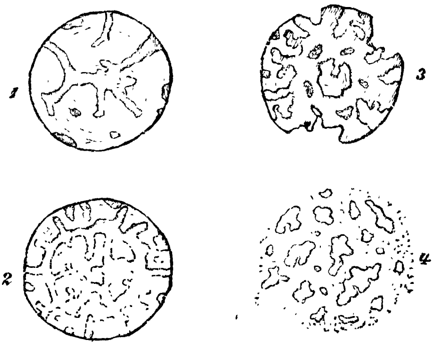

FIG. 247.—Different stages of the corrosion shown by the starch-grains of germinating Barley. (After NOLL.)

Cellulose is also of frequent occurrence as a reserve substance (54). In the endosperm of many seeds the cell-walls are very strongly thickened and the thickening layers, which consist of hemicelluloses, are dissolved in the process of germination. Such thickened walls are beautifully shown in many palm seeds, *e.g.* in the Vegetable Ivory Palm. The solution of the thickening is due to an enzyme, the so-called cytase, which, however, does not act on every variety of cellulose. Typical cellulose (p. 35) is not attacked by it, but is acted on by another enzyme, cellulase.

Inulin, which is found especially in Compositae and Campanulaceae, originates in the same way from fructose as starch does from maltose (54), but is distinguished from starch by always occurring in plants in the dissolved form. In spite of this it is incapable of translocation on account of the size of its molecule, and is broken down on germination by an enzyme (inulase) into fructose.

Cane Sugar is stored in quantity as a reserve substance, for example in the sugar-cane and sugar-beet. It is converted by the widely-spread enzyme "invertase" or saccharase into equal parts of dextrose and levulose.

2. The Fats

Though we are unable to manufacture the reserve carbohydrates mentioned either from dextrose or levulose, we can understand that it is as easy for the plant to build them up as to break them down. It is much more difficult to understand in what way the plant is able to form fats (glycerol esters of various fatty acids; cf. p. 28) from carbohydrates. Fats are always present in living protoplasm. They occur in relatively large amounts as reserve materials, but not in the assimilating foliage leaves. They occur in large amount in many ripe seeds, where they are formed at the expense of carbohydrates. At germination they are decomposed by the enzyme lipase into fatty acids and glycerol. The fatty acid is capable of passing through the water-saturated cell-wall more readily than the fat, but does not usually travel as such for any considerable distance in the plant; it is usually quickly converted into a carbohydrate ([54a]).

3. Albuminous Substances

Albumin occurs in the storage places for reserve materials partly dissolved and partly in a crystalline or an amorphous form. The crystals occur free in the cytoplasm, nucleus, or in the chromatophores (cf. Fig. 27 *B*, *kr*); in seeds they are found especially in the aleurone grains, where they are associated with globoids (cf. p. 29).

The products of the hydrolytic breaking down of albuminous substances are mainly amino-acids, the wide distribution of which in the plant has already been referred to. When seeds rich in protein such as *Ricinus*, *Pinus*, etc., are germinating, the abundant amino-acids may be regarded as derived from the protein. Amino-acids occurring in other situations may have arisen in the synthesis of proteins. The protein-molecule does not produce at once or exclusively amino-acids; the breaking down of the very large molecule is a gradual one, in which the bodies which appear first have many properties in common with proteins; first comes albumose, then peptone, and only then amino-acids. With the latter appear ammonia, also products of decomposition containing sulphur and phosphorus, and generally carbohydrates also.

This hydrolytic breaking down of proteins takes place under the influence of "proteolytic" enzymes (proteases) which very probably are closely similar to corresponding enzymes in the animal body. We should therefore have to distinguish:

1. Pepsin, which only breaks down the protein molecule to albumoses and peptone.
2. Erepsin, which transforms peptone into amino-acids.
3. Trypsin, which transforms proteins directly into amino-acids.
4. Amidase, which splits ammonia from amino-acids.

The decomposition products of albumin quickly undergo changes in the plant, and therefore the mixture of nitrogenous organic compounds which one obtains from a plant kept in the dark is not identical with the products of the hydrolysis of albumin outside the plant. In the plant syntheses take place after the primary decomposition, and these lead to the formation of such substances as amides, the most widely spread of which is asparagine. This dominates in Gramineae and Leguminosae (15 g. are present in a litre of sap from bean seedlings); it is replaced in Cruciferae and Cucurbitaceae by glutamin, while in the Coniferae a di-amino-acid (arginin) appears to play the same part. Such syntheses mainly serve to avoid the presence of poisonous ammonia (51). The formation of amides in plants thus corresponds to a certain extent with that of urea in animals. Asparagine and urea both represent ammonia in a non-poisonous form. The animal which readily obtains nitrogen in its food without expenditure of energy can afford to continually excrete it. On the other hand the plant which only assimilates nitrogen with difficulty preserves the asparagine for future use. The syntheses proceed still farther in light, when protein may again be formed from the products of decomposition of albumin.

B. TRANSPORT OF THE MOBILISED RESERVE MATERIALS

When the reserve materials have been brought by the aid of the proper enzymes into the soluble form, or have been transformed into substances with smaller molecules, they are capable of being transported; we may speak of them as being mobilised. Their movements are governed by the general principles of translocation of substances. It is especially necessary that a diffusion current should be established and maintained. This may be brought about by the active growth of cells at a greater or less distance from the place of storage of the reserve material. As long as this lasts each molecule on its arrival at the place of growth is promptly transformed (*e.g.* sugar into cellulose), and thus room is made for the molecules that follow. In non-growing organs also (*e.g.* cotyledons, endosperm) a gradient of diffusion is established by the cells to which the current passes having a greater power of condensing the sugar (forming starch) than the others. A diffusion current can also be artificially established where a storage structure under proper conditions is placed in relation on one side with a large amount of water. It is thus possible to bring about artificially an emptying of seeds, bulbs, etc.

All movements of diffusion proceed slowly. For example, a milligramme of Na Cl requires at least a year in order to diffuse from a 10 per cent solution to a distance of 1 metre. The same amount of cane sugar would take 2½ years, and other substances diffuse still more slowly. Thus, when substances have to be transported for considerable distances, the movement of diffusion, since it goes on so slowly, is replaced by movement in mass. In spring the reserve materials deposited in the wood of our trees are carried up by the ascending current of water in the vessels ; at this season the fluid in the vessels contains abundant glucose. In the other direction a stream of mobilised reserve material can pass downwards from the foliage leaves by way of the sieve-tubes. While, however, the mechanical causes of the transpiration stream are at least partially understood, so far as they depend upon the evaporation of water, we do not know the forces concerned in movements in mass in the sieve-tubes (55).

Another example of translocation is afforded by leaves before they are shed. Shortly before the leaf-fall the leaves turn yellow ; while the green pigments of the chlorophyll are dissolved and carried away, the yellow pigments remain in the chloroplasts. In many but not all cases the useful materials in the leaf are transferred to the stem and thus are not lost to the plant. Phosphoric acid, potassium, and nitrogenous substances are thus transferred to the stem, but the cell-walls, a protoplasmic layer, and osmotically-active substances in the vacuole remain so that the leaf falls in a turgescent condition (56).

C. FURTHER METAMORPHOSES OF SUBSTANCE

Regeneration of Reserve Materials.—Sooner or later the reserve materials mobilised by the help of enzymes are again converted into substances with large molecules. This occurs at any rate at the end of their transport, whether they are again deposited as reserve materials or are employed as constructive substances. Thus, for example, glucose formed in a leaf may pass to a seed or a tuber and be there transformed into starch or cell-wall. When the transport is for a considerable distance the formation of reserve material may go on by the way and not only at the end of the journey. This is specially well seen in the case of starch. Along the routes of sugar-transport so-called transitory starch may be formed in every cell. This starch-formation diminishes the concentration of the solution, and thus helps to maintain the continued motion of the diffusion current (56a).

Other Products of Metabolism (57).—Only a small proportion of the substances met with in plants have been enumerated above. It will be sufficient to mention here the organic acids, tannins, glucosides, alkaloids, colouring matters, ethereal oils, resins, gum-resins, caoutchouc and gutta-percha among the legion of substances which are derived from the products of assimilation. The organic acids will be referred to later (p. 266); the origin and physiological significance of the others are too little known for them to be dealt with. It is known that as a rule they are not further utilised after their formation. They are probably, therefore, by-products and end-products of the metabolism of the plant.

They need not, however, for this reason be useless, and it is believed that some bitter or poisonous substances protect the plant from being eaten by animals; some pigments are of use in the attraction of animals which distribute pollen, seeds, and fruits, or frighten away injurious animals (warning-colours). Resin and latex when they exude and harden may assist in the closing of wounds.

The Ripening of Succulent Fruits.—A striking transformation of substances takes place in the ripening of succulent fruits. The change of starch into sugar associated with the disappearance of organic acids and tannins is of frequent occurrence. The fruits thus become sweet-tasted instead of acid or bitter, and are eaten by animals which distribute the seeds. The significance of these chemical changes is thus ecological.

VII. Heterotrophic Nutrition

The considerations in the preceding pages have had reference to the green plant, which forms the organic substances required for its construction and metabolism from purely inorganic materials. Such plants are termed AUTOTROPHIC. In contrast to them are those plants which require organic nutrient materials and are therefore dependent in their nutrition on the activity of other organisms (cf. pp. 156, 178); these are termed HETEROTROPHIC plants.

The metabolism of heterotrophic plants is in general respects not essentially different from that of autotrophic plants. This is evident when it is considered that many of the cells of the latter have "heterotrophic" nutrition. The entire root-system in the soil, for instance, is unable to construct carbohydrates but must obtain them from the green subaerial portions of the plant. It is indeed only the green parts of the above-ground organs which can assimilate the carbon dioxide of the air, and the colourless portions are dependent on them. When a plant as a whole has assumed a heterotrophic mode of nutrition, this implies a loss of certain nutritive functions but not a new kind of metabolism. It has been pointed out in the morphological section (p. 178) how these functional changes find expression in the external form of heterotrophic plants.

Heterotrophic plants are distinguished as saprophytes and parasites according to the source of their organic nutrient materials. The former live on dead organic material, while parasites obtain their food from living organisms.

Saprophytes.—The demands which heterotrophic plants make on sources of carbon and nitrogen can be best studied in saprophytic bacteria and fungi. These organisms can be cultivated on various complex substrata, and conclusions can be drawn from their growth as to the nutritive value of the compounds supplied as food. In order first to ascertain the sources of carbon the nutrient solution must contain, in addition to the indispensable mineral substances, a source of nitrogen, usually ammonium nitrate; to this various sources of carbon can be added. It should have a slightly acid reaction for mould fungi and be weakly alkaline or neutral for bacteria; such cultures show that sugars are very good food-materials. The sugar can, in many cases, be more or less suitably replaced by other organic substances such as other carbohydrates, certain alcohols, fats, albumin and derived substances, organic acids, etc. While these sources of carbon can be placed in order as regards their nutritive value for any particular organism, this cannot be done generally; there are many saprophytes which are adapted to quite peculiar conditions and use in preference, as a source of their carbon supply, compounds which for the majority of other plants have scarcely any nutritive value (*e.g.* formic acid, carbonic acid, oxalic acid).

Even the saprophytes which succeed on very various compounds of carbon (omnivorous saprophytes) are capable of distinguishing between them. Thus from ordinary tartaric acid *Penicillium* only utilises the dextro-rotatory form, and certain bacteria only the laevo-rotatory form. *Aspergillus* growing in a mixture of glucose and glycerol utilises the former first ("selection" of nutritive materials). If the glycerol alone is given, it is completely utilised.

As regards the nitrogenous food supply the facts are not so clear as for the carbon compounds. Culture experiments have shown that some saprophytes prefer this in the form of nitric acid; as a rule, however, ammonium salts afford the best inorganic source of nitrogen. It is often stated that some fungi will not succeed with such relatively simple nitrogenous compounds, or at least that they construct the nitrogenous substances of their bodies with greater ease and certainty from organic compounds of nitrogen. Since, however, there are many sources of error in such investigations that have to be considered, the whole question requires re-examination (58).

Most heterotrophic plants have cells limited by firm walls, and can only absorb substances in solution. Since these are only rarely available for them under natural conditions the power which many of these plants possess of excreting enzymes which can render solid food-materials soluble, is of great importance. If, for example, a mould-fungus is grown on starch-paste it will excrete diastase, which acts on the starch outside the cell and converts it into sugar which can then be absorbed.

The various fungi and bacteria have quite specific enzymes. Most of them cannot attack the resistant cellulose, but certain bacteria can secrete enzymes which break it down and so can use cellulose as their most appropriate food-material.

Such requirements explain many of the far-reaching decompositions which various organic substances undergo in the decompositions and putrefactions brought about by saprophytes. These generally distributed biochemical processes can be regarded as digestive processes, corresponding to those that take place in the intestines of animals.

Parasites.—Phanerogamic plants such as *Rafflesia* and *Cascuta* which have been described on pp. 178 ff. are completely heterotrophic. In their metabolism they behave as do the colourless cells and tissues of their host-plants; they obtain organic compounds from the leaves of the host and also derive their nutrient salts from the roots of the latter.

The heterotrophy is not always, as in those cases, complete. Frequently it applies to only one of the two main syntheses in metabolism. Thus some heterotrophic Phanerogams can construct their organic carbon-compounds in the normal fashion from carbon dioxide, while they are heterotrophic as regards their nitrogenous requirements. The converse case is frequently met with.

There are certain micro organisms which are strikingly autotrophic as regards nitrogen, while they are heterotrophic as regards their carbon assimilation. These organisms are able to utilise the nitrogen of the atmosphere. Their existence was first established at the end of last century by the work especially of WINOGRADSKY, HELLRIEGEL, and WILFARTH (59).

In the first place there are certain Bacteria, such as *Clostridium Pasteurianum* and related forms and *Azotobacter chroococcum*, which live independently in cultivated soil and in water under very various external conditions. They fix free nitrogen and thus possess a very important power both for their own success and for that of many other organisms; this property is of the greatest importance in agriculture. An increasing number of the lower Fungi have been shown by recent researches to have the same power though in less degree. In addition to these free-living forms there are micro-organisms which occur within higher plants and have the same property. The best investigated among these are the various forms of *Bacillus radicicola*, which infest the roots of Leguminosae and frequently give rise to enormous numbers of gall-like tubercles upon them (Figs. 248, 249). This appears to be a case of mutualistic parasitism, a living together of organisms to their mutual benefit, such as was termed by DE BARY symbiosis. The Leguminosae thus appear to differ from all other green plants in their mode of accumulating nitrogen (60); this was first established by GILBERT and LAWES in England and SCHULTZ-LUPITZ in Germany.

The rod-shaped bacteria penetrate through the root-hairs into the cortex of the roots, and there give rise to the tubercles. These tubercles become filled with a bacterial mass, consisting principally of swollen and abnormally-developed (hypertrophied) BACTERIOIDS, but in part also of bacteria which have remained in their normal condition. While the bacteria live on carbohydrates and at first also on albuminous substances supplied by the host plant, the latter profits by the power of fixing free nitrogen possessed by the bacterioids. The bacterioids furnish a steady supply of combined nitrogenous substance to the leguminous plant. It has been calculated that Lupins are able in this way to obtain 200 kg. of nitrogen per hectare. The agricultural importance of this natural fixation of nitrogen will be evident. It has been attempted to further it by infecting fields with soil rich in the bacteria or with pure cultures of specially active forms. A marked increase in the crop of *Serradella* is obtained in this way. If the soil in which a leguminous plant is grown contains a sufficiency of nitrates, the plants may live at their expense ; since the presence of nitrates exerts an injurious influence on *Bacillus radicicola*, practically no nodules are formed under such circumstances.

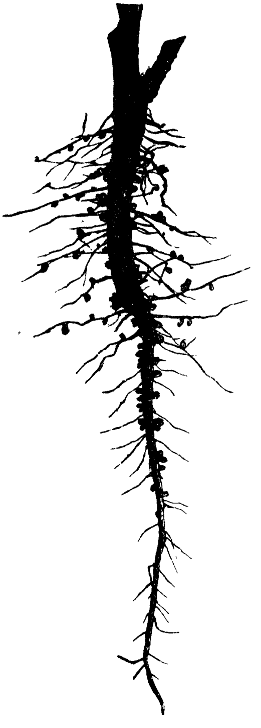

FIG. 248.—A root of *Vicia Faba*, with numerous root-tubercles. (Reduced. After NOLL.)

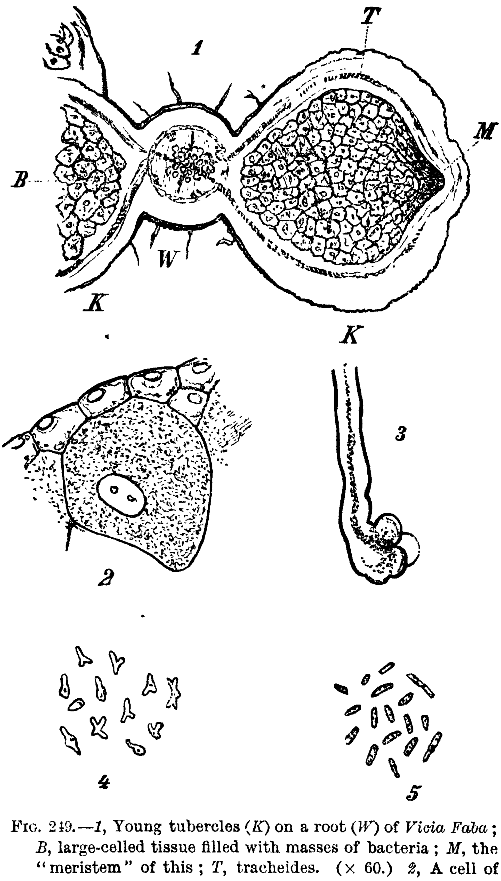

FIG. 249.—*1*, Young tubercles (*K*) on a root (*W*) of *Vicia Faba* ; *B*, large-celled tissue filled with masses of bacteria ; *M*, the "meristem" of this ; *T*, tracheides. (× 60.) *2*, A cell of the tubercle filled with thousands of bacteria, and beside it some uninfected cells. (× 320.) *3*, An infected root-hair containing the "infection thread." (× 320.) *4*, Bacteroids. *5*, Unaltered bacteria. (× 1200. After NOLL.)

Root-nodules are regularly produced, owing to infection by lower organisms, in *Alnus*, *Elaeagnus* and *Casuarina*. *Elaeagnus* and *Alnus* are able to assimilate the free nitrogen of the atmosphere when their roots are thus provided with nodules. *Podocarpus* has the same power, but in this case there is an association of a fungus with the root, a mycorrhiza (61).

A MYCORRHIZA is met with in many plants, especially those that live in woods and heaths. The two extreme forms, between which intermediates exist, are termed

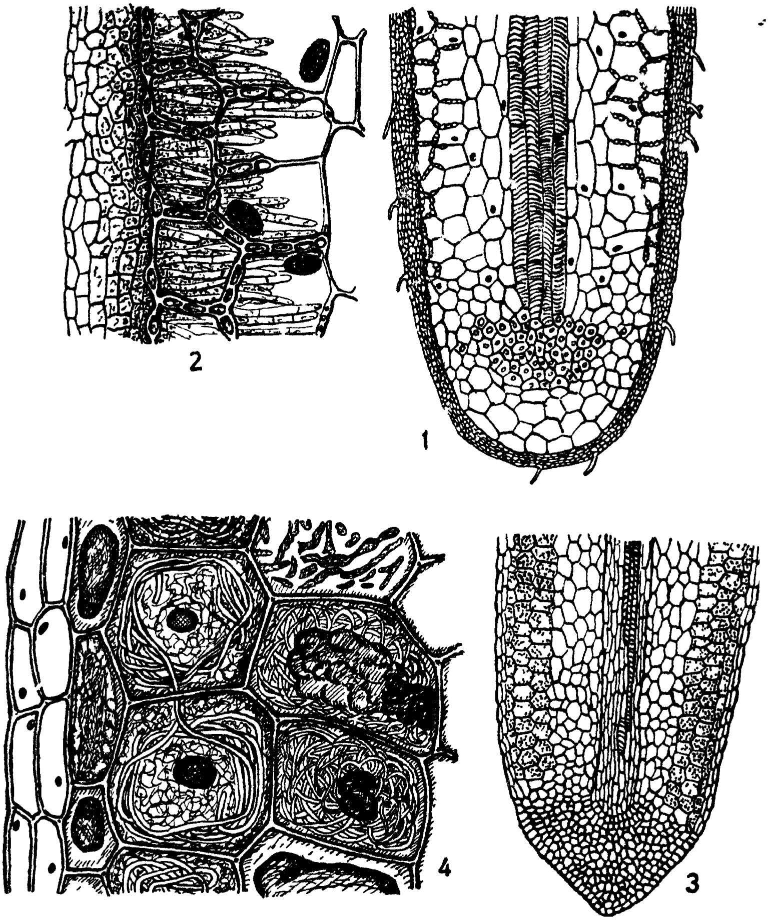

FIG 250.—1. Longitudinal section through the root-tip of *Pinus sylvestris*, with ectotrophic mycorrhiza (magnified). 2. Part of Fig. 1, more highly magnified, showing hyphae from the external covering of fungus penetrating between the cells of the root. 3. Longitudinal section of the root tip of *Neottia*. The three layers of cells with dark contents are those inhabited by fungal hyphae (endotrophic mycorrhiza) (magnified) 4. Part of Fig 3 more highly magnified, showing details of the fungus The middle layer inhabited by fungus consists of host cells in which the fungus survives; in the outer and inner layers the fungus is digested. (After WERNER MAGNUS, from KNY, Wandtafeln)

ECTOTROPHIC and ENDOTROPHIC mycorrhiza. In the former (Fig. 250, 1, 2) the root has a covering of fungal hyphae which extends over the growing point; this occurs in many trees and in *Monotropa*. The fungus in the case of endotrophic mycorrhiza (Fig. 250, 3, 4) inhabits the cells of certain layers of the root, and only sends out isolated hyphae into the soil (Orchidaceae, Ericaceae, many Liliaceae). The fungus of endotrophic mycorrhiza is in part digested by the cells of the root, and the materials thus obtained from it are available for the host plant. Though it is not established with certainty that the fungus can fix free nitrogen, the endotrophic mycorrhiza is to a certain extent explained. It is also known to be in some cases indispensable ; thus, when the fungus is wanting, germination frequently does not take place in Orchidaceae, and in Ericaceae the further development of the seedling is arrested. The relations between the plant and ectotrophic mycorrhiza are not so clear ; there are several unconnected explanations. According to one the fungus is a pure, harmful parasite, while according to another the flowering plant is parasitic on the fungus. A third view assumes a true symbiosis between the two organisms, and represents, following STAHL, the connection between the two in the following way. The fungus absorbs nutrient salts energetically from the soil and supplies the autotrophic plant with them ; in return this supplies the fungus with organic food. Since, however, an ectotrophic mycorrhiza occurs in certain colourless Phanerogams (*e.g. Monotropa*), there must, in these cases at least, be a parasitism of the flowering plant on the fungus. The same holds for the non-green Orchids that contain endotrophic mycorrhiza (*Neottia, Coralliorhiza, Epipogon*) ; these plants are not living saprophytically on the humus, but are evidently dependent on the mycorrhiza fungus for their nutrition.

The communal life of Algae and Fungi which is found in the case of Lichens evidently comes under the third of the explanations suggested for ectotropic mycorrhiza (62).

More recently, swellings which are due to infection by bacteria have been discovered in the leaves of tropical plants belonging to the Rubiaceae and Myrsinaceae. While, however, in the case of the Leguminosae the infection always depends on accidental meeting of the bacteria and the flowering plant, in these families the bacteria are present in the embryo of the plant. When they are artificially kept from the egg-cell the development of *Ardisia* is abnormal. It is established, at least in the case of the Rubiaceae, that an assimilation of free nitrogen takes place (63).

Semi-parasites.—The last-mentioned heterotrophic plants lead to the consideration of others which, while possessing green leaves rendering them capable of active assimilation, have special organs to obtain nitrogenous organic materials (64). Our native Mistletoe, which lives on trees, and many exotic Loranthaceae, have well-developed leaves so abundantly provided with chlorophyll that they suffice to supply all the carbohydrates needed ; these plants, however, obtain water and nutrient salts from the host plant. In correspondence with this their root-system is reduced.

Other plants can only develop normally when their root-system is connected to that of other plants by means of haustoria. This is the way in which *Thesium* (Santalaceae) and many Rhinanthaceae live. It is not yet known in what form they obtain their nutrient salts from the host-plant.

Insectivorous Plants.—The so-called INSECTIVOROUS or CARNIVOROUS PLANTS must be referred to here (65) (cf. p. 175 f). These are plants provided with arrangements for the capture and retention of small animals, especially insects, and for the subsequent solution, digestion, and absorption of the captured animals by means of enzymes. All these insectivorous plants are provided with chlorophyll; the explanation of their peculiar mode of life can hardly be to obtain organic compounds of carbon. It is further known that they can succeed without animal food, but the moderate supply of an animal substance has a distinctly beneficial effect, manifested in increased production of fruits and seeds. It is very probable, though by no means established, that the carnivorous habit is a means of obtaining nitrogen. Whether the nitrogen in the peat or water in which insectivorous plants often grow is insufficient in quantity, or whether its quality is not optimal, must be left undetermined. It is doubtless possible that organically-combined nitrogen is specially advantageous to these plants. This does not exclude the possibility that the insectivorous habit is related not only to the supply of nitrogen, but to that of other nutrient salts, especially of potassium and phosphoric acid. Whether these salts are utilised in organic combinations or are transformed in the digestive process to the inorganic form is unknown. In the latter case the use of the insectivorous habit would have to be sought in the provision of a larger supply of nutrient salts than is afforded by the soil.

The insectivorous plants strike the ordinary observer as deviating from ordinary plants in the direction of the animal kingdom. Like animals they utilise solid food which has to be rendered fluid by enzymes before it is absorbed into the cells. The similarity between animals and these plants appears to be increased by a comparison with the stomach of the pitchers, etc., of some insectivorous plants. It should be recognised, however, that some Fungi and Bacteria stand physiologically closer to animals. They can obtain all their food by the digestion of solid organic material, while the insectivorous plants are autotrophic, at least as regards their supply of carbon.

VIII. Respiration and Fermentation

In the higher plants all the organic substance produced in assimilation is not used for purposes of construction and storage; a part of it is always broken down and returns to the state of inorganic compounds. Along with assimilation there is always DISSIMILATION. The significance of this process, which is usually associated with the absorption of oxygen and is termed RESPIRATION, does not lie in the substances formed but in the LIBERATION OF ENERGY which is essential for the life of the plant. In certain lower plants the necessary supply of free energy may sometimes be obtained in other ways; usually organic substances are absorbed from the substratum and broken down without being first assimilated. The decomposition may be effected by oxidation, reduction, or dissociation; all these processes are grouped together as FERMENTATION. Other lower organisms isolated hyphae into the soil (Orchidaceae, Ericaceae, many Liliaceae). The fungus of endotrophic mycorrhiza is in part digested by the cells of the root, and the materials thus obtained from it are available for the host plant. Though it is not established with certainty that the fungus can fix free nitrogen, the endotrophic mycorrhiza is to a certain extent explained. It is also known to be in some cases indispensable; thus, when the fungus is wanting, germination frequently does not take place in Orchidaceae, and in Ericaceae the further development of the seedling is arrested. The relations between the plant and ectotrophic mycorrhiza are not so clear; there are several unconnected explanations. According to one the fungus is a pure, harmful parasite, while according to another the flowering plant is parasitic on the fungus. A third view assumes a true symbiosis between the two organisms, and represents, following STAHL, the connection between the two in the following way. The fungus absorbs nutrient salts energetically from the soil and supplies the autotrophic plant with them; in return this supplies the fungus with organic food. Since, however, an ectotrophic mycorrhiza occurs in certain colourless Phanerogams (*e.g. Monotropa*), there must, in these cases at least, be a parasitism of the flowering plant on the fungus. The same holds for the non-green Orchids that contain endotrophic mycorrhiza (*Neottia*, *Coralliorhiza*, *Epipogon*); these plants are not living saprophytically on the humus, but are evidently dependent on the mycorrhiza fungus for their nutrition.

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A. RESPIRATION

By respiration in its typical form is understood the oxidation of organic material to carbon dioxide and water; this involves the absorption of oxygen from without (cf. p. 237).

In the higher animals the process of respiration is so evident as not easily to escape notice, but the fact that plants breathe is not at once so apparent. Just as the method of the nutrition of green plants was only discovered by experiment, so it also required carefully-conducted experimental investigation to demonstrate that PLANTS ALSO MUST BREATHE IN ORDER TO LIVE; that, like animals, they take up oxygen and give off carbonic acid. The question had already been thoroughly investigated by SAUSSURE, and by DUTROCHET in the years 1822 to 1837, and its essential features correctly interpreted. Later the existence of respiration in plants was doubted, owing to the demonstration of their power of decomposing carbon dioxide and giving off oxygen; it seemed impossible that both processes could go on at the same time. The correct view was then formulated by SACHS. ASSIMILATION AND RESPIRATION ARE TWO DISTINCT VITAL PROCESSES CARRIED ON INDEPENDENTLY BY PLANTS. WHILE IN THE PROCESS OF ASSIMILATION **GREEN** PLANTS ALONE, AND ONLY IN THE LIGHT, DECOMPOSE CARBONIC ACID AND GIVE OFF OXYGEN, **ALL** PLANT ORGANS, WITHOUT EXCEPTION, BOTH BY DAY AND BY NIGHT, TAKE UP OXYGEN AND GIVE OFF CARBONIC ACID. Organic substance, obtained by assimilation, is in turn lost by respiration. That green plants growing in the light accumulate a considerable surplus of organic substance is due to the fact that the daily production of material by the assimilatory activity of the green portions is greater than the constant loss which is caused by the respiration of all the organs. Thus, according to BOUSSINGAULT'S estimates, a plant of Sweet Bay in the course of one hour's assimilation will produce material sufficient to cover thirty hours' respiration. If assimilation is suppressed by keeping the plant in darkness, it loses considerably in dry weight.

Plants produce in twenty-four hours about five to ten times their own volume of carbonic acid. In shade-plants this is usually reduced to twice the plant's volume, while the commonly-cultivated *Aspidistra* produces only one-half of its own volume, and can therefore succeed even under conditions of dim light which are unfavourable to assimilation.

In order to demonstrate the existence of respiration either the absorption of oxygen or the giving off of carbon dioxide by the plant may be employed. If a handful of soaked seeds is placed at the bottom of a glass cylinder, the top of which is closed for a day by a glass plate, the oxygen in the space is used up by the germinating seeds; a candle will be extinguished if it is introduced into the cylinder. If germinating seeds, or flower-heads of Compositae (B, Fig. 251) or young mushrooms are placed in a flask and prevented from falling out when the flask is inverted by means of a plug of cotton-wool (W), the mouth of the flask can be dipped under mercury (S) and some solution of caustic potash (K) be introduced above this. The carbon dioxide formed is then absorbed by the caustic potash and the mercury rises (Fig. 251). When this experiment is carried out quantitatively it is found that a fifth of the volume of air disappears, so that all the oxygen has been absorbed. Since, however, when no potash is present, the volume of gas is not altered by the respiration of the plants, an equal volume of carbon dioxide must be formed for each volume of oxygen that is absorbed. The respiratory coefficient, or ratio between the absorbed oxygen and the excreted carbon dioxide, is equal to unity $\left(\frac{CO_2}{O_2} = 1\right)$. If we assume that a hexose is the substance respired, this must take place according to the formula

$$C_6H_{12}O_6 + 6O_2 = 6CO_2 + 6H_2O$$
$$+ 674{,}000 \text{ gramme calories.}$$

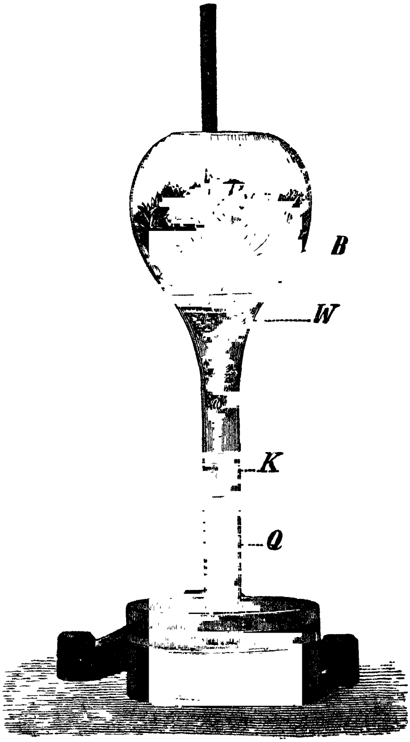


FIG 251.—Experiment to demonstrate respiration. The inverted flask (*B*) is partially filled with flowers which are held in place by the plug of cotton (*W*) Owing to the absorption of the carbon dioxide exhaled in respiration by the solution of caustic potash (*K*), the mercury (*Q*) rises in the neck of the flask. (After NOLL.)

The gain in energy is thus very considerable. In this process, which is exactly opposite to the assimilation of carbon dioxide, it is not so easy to demonstrate the formation of water as it is to show the utilisation of oxygen and the production of carbon dioxide. Quantitative estimates of the loss of dry weight and of the carbon dioxide formed show that the latter does not account completely for the former; a part of the dry substance must thus have been transformed into water since no gases other than CO_2 are produced.

The volume of air does not under all circumstances remain unchanged by the respiration of the plant; the carbon dioxide produced is not always equal in volume to the oxygen which disappears. Small deviations from this ratio occur in all plants, and considerable ones in, for instance, the germination of fatty seeds, and in the leaves of certain succulent plants (Crassulaceae). This is connected with the fact that in these seeds fats, which are much poorer in oxygen than carbohydrates, are used in respiration; and that in the Crassulaceae certain organic acids are produced from carbohydrates, instead of carbon dioxide and water. In other plants also similar acids, though not in so great amount, are formed. They probably arise mainly in the respiratory process, but may also be produced in constructive metabolism. Oxalic acid, the wide distribution of which as calcium oxalate is well known, must particularly be mentioned. Its production is proportional to its neutralisation by calcium; if this does not take place its production is diminished. Even in plants that do not contain calcium oxalate, there is a production of oxalic acid which is then rapidly oxidised further.

In the germination of fatty seeds far more oxygen is absorbed than carbon dioxide is given off; this may go so far that in the first days in the dark, in spite of continual respiration, an increase in the dry weight takes place. The respiratory quotient is thus less than 1. Most of the oxygen is used in the transformation of fats, which are poor in oxygen, into carbohydrates, and only a small proportion is used in respiration.

In the Crassulaceae a large proportion of the carbohydrate is changed into organic acids in the process of respiration. The oxidation is thus incomplete; it does not lead to the formation of CO_2, so that less of this gas is formed than the amount of oxygen absorbed would lead us to expect. The respiratory quotient is less than 1. This peculiar respiratory process which is connected with an accumulation of acids in the cell-sap, as can be recognised by the taste, is of great ecological significance for succulent plants. The acids formed (especially malic and oxalic acids) give off CO_2 in the light. This can be again employed in assimilation, while, in typical respiration at least, the CO_2 formed during the night escapes, and is lost to the plant. The succulents thus economise their supply of C, which is probably connected with the fact that they do not so readily obtain carbon dioxide from the air as other plants, owing to the diminution of gaseous exchange on account of the limitation of transpiration (66).

As has been mentioned, respiration is of general occurrence in the higher plants. It not only occurs in the parts of plants which do not possess chlorophyll and are commonly used in experiments on respiration, but can be demonstrated also in cells which contain chlorophyll. In this case the respiration in the light is masked by the quantitatively greater process of assimilation; it appears only as a diminution in the products of assimilation. If the light is diminished assimilation ultimately ceases and the respiration becomes evident.

Though respiration goes on in every living cell its intensity varies greatly in different organs and under various external conditions.

Actively-growing parts of plants, young fungi, germinating seeds, flower-buds, and especially the inflorescences of Araceae and Palms, exhibit very active respiration. In some bacteria and fungi this exceeds, as compared with the body-weight, the respiration of the human body. In most cases, however, especially in parts of plants composed wholly or mainly of full-grown tissues, the consumption of oxygen and production of carbon dioxide is considerably less than in warm-blooded animals. Among external conditions which have an important influence on the intensity of respiration the temperature and the amount of oxygen must be especially mentioned. An increase of temperature accelerates respiration as it does all the vital processes. The production of carbon dioxide is about doubled or trebled by a rise of 10° C., just as other chemical processes outside the plant are. With continued rise of temperature, however, the respiration diminishes. In contrast to other like phenomena the fall in the respiratory curve is exceedingly steep, so that the optimum and maximum almost coincide.

Respiration is commonly spoken of as a process of combustion. Were this correct it might be expected that the amount of available oxygen would be of fundamental importance; in particular it might be anticipated that respiration would be greatly increased in pure oxygen and completely suspended in a space free from oxygen. Neither of these assumptions is true. Respiration is not markedly increased in pure oxygen, and only at a pressure of 2-3 atmospheres of oxygen does an increase in the respiration become perceptible; this is soon succeeded by a decrease in the respiration indicating the approach of death. Even more striking is the fact that plants in the absence of oxygen continue to produce carbon dioxide. In this case one cannot speak of a process of combustion; the phenomenon is termed INTRAMOLECULAR RESPIRATION (^{67}) because the carbon dioxide which is formed owes its origin to a rearrangement of the atoms in the molecule of the sugar which serves as the material for respiration. The molecule of sugar breaks down and forms, in addition to carbon dioxide, other reduced compounds, sometimes, for example, alcohol according to the formula

$$C_6H_{12}O_6 = 2C_2H_6O + 2CO_2 + 28{,}000 \text{ gramme calories.}$$

If this empirical formula is replaced by the structural formula

$$\begin{gathered} COH\,.\,CHOH\,.\,CHOH\,.\,CHOH\,.\,CHOH\,.\,CH_2OH \\ = CO_2 + CH_3\,.\,CH_2OH + CH_3CH_2OH + CO_2, \end{gathered}$$

it will be seen that the molecule of sugar has broken down into four portions, two of which are poorer and two richer in oxygen than the molecular groups from which they are derived. In this type of respiration certain molecular groups withdraw the combined oxygen from others. The above equation further shows that the gain in energy per gramme molecule of utilised glucose is much less in intramolecular than in ordinary respiration; 28,000 gramme calories as compared with 674,000.

It may be assumed that oxygen-respiration and intramolecular respiration are expressions of one and the same property of the plant; in other words, that on withdrawal of oxygen normal respiration passes over into intramolecular respiration. If this is true, it follows that the essence of respiration does not consist in an oxidation process but in a breaking down of organic substance in which products arise that readily take up oxygen. The materials which are respired in the plant, such as carbohydrates and protein, are not easily oxidisable at ordinary temperatures. Fats, it is true, which may also serve as material for respiration, are oxidisable, but in this case we know that they are transformed into carbohydrates before they are used for respiration by the plant. The plant must thus have at its disposal special means in order to carry on the oxidation of the substances that are involved in respiration.

In recent years two well-founded conceptions of the chemistry of respiration have been developed by WIELAND and WARBURG (68). It can now be assumed that the primary process in the combustion of the material of respiration does not consist in an activation of oxygen in the sense of the formation of ozone or hydrogen peroxide. Were this so, numerous substances in the cell would be oxidised by O_3 or H_2O_2 and there could not be a selective combustion, easily oxidisable substances being avoided and those more difficult of oxidation attacked.

According to WIELAND the primary process in respiration consists in an introduction of water into the respiratory material, *e.g.* sugar. Following on this an oxidation, determined by enzymes, and progressing by a number of stages, takes place; this takes the form of a withdrawal of hydrogen and a simultaneous setting free of CO_2. WIELAND was able to show that glucose in the presence of the catalyst, palladium black, at ordinary temperatures gives off H and CO_2 if oxygen is excluded. The hydrogen is absorbed by the palladium black so that the process becomes weaker as the palladium becomes saturated with hydrogen; it proceeds, however, in the presence of an acceptor of hydrogen. In the absence of air, methylene blue will act in this way, forming a colourless compound; on access of air the oxygen takes on this rôle and water is formed.

In higher plants the place of the palladium-black is taken by certain enzymes which transfer the hydrogen of the addition-compound of the sugar and water to readily reducible substances. These H-acceptors have been named respiratory pigments by PALLADIN. From the respiratory pigments the hydrogen is then transferred by the action of the so-called OXIDASES to the atmospheric oxygen, and as a result water is produced. Thus the oxidases, which are also enzymes, do not convey the atmospheric air to the sugar but to the hydrogen which has been liberated from the sugar in the manner described above. The general presence of oxidases in plants has been demonstrated.

The following outline scheme represents the respiration of sugar.

$$\begin{array}{lrcl}
1. & C_6H_{12}O_6 + 6H_2O & = & 6CO_2 + 24H \\
2. & 24H + 6O_2 & = & 6H_2O + 6H_2O \\
\hline
 & C_6H_2O_6 + 6O_2 & = & 6CO_2 + 6H_2O
\end{array}$$

If free oxygen is wanting the reaction must take another course. Either, as in some fermentations (p. 270), the hydrogen will be given off as such, or it will be used in the formation of less highly oxidised products of combustion, *e g.* alcohol. In all probability there will first arise in the respiration of the sugar those substances which will be mentioned below in connection with alcoholic fermentation.

The second theory, developed by WARBURG, starts from the fact of experience that the material of respiration cannot be oxidised in a solution either by oxygen alone or in the presence of oxidases. Protoplasm is, however, not a true solution but contains numerous particles that can be regarded as solid. Since the multitude of these particles possess a very large surface all reactions in the cell that take place at surfaces are greatly promoted. The particles of the protoplasm further contain iron in the ionised form. Iron is known to greatly hasten the transference of oxygen to oxidisable bodies. THE MATERIALS FOR RESPIRATION ARE OXIDISED AT THE SURFACES OF THE PARTICLES IN THE PRESENCE OF CATALYTICALLY ACTIVE IONS OF IRON. The cause of the combustion in living cells is, according to WARBURG, the adsorption of the respiratory material, along with oxygen, on the iron-containing surfaces.

It is impossible to decide at present which of these two theories is correct, and whether respiration does not proceed sometimes according to the one and sometimes according to the other.

At first sight respiration appears a contradictory process, since in it organic material which has been built up in assimilation is again broken down. Its meaning only becomes evident when, turning from the changes of substance, those of energy are considered. It is not the production of CO_2 and H_2O that is important, but only the liberation of energy. This is effected on the breaking down of such substances as carbohydrates, for the construction of which, as has been seen, a supply of energy is requisite. On this liberated energy the plant is dependent for the driving force in many of its vital phenomena. Movements of protoplasm, growth, and movements due to stimuli cease on the withdrawal of oxygen from the plant. All these vital phenomena begin again on the restoration of a supply of oxygen, if this is not too long delayed. It might have been expected that the organism would possess arrangements by the help of which the external energy of light or heat could be employed as driving power. Practically, however, it is found that the plant proceeds to store up the energy of the sun's rays in the form of potential chemical energy, and then utilises this at need. This method has the great advantage that the stored energy can be very easily carried to other places in the plant. It can thus reach, for example, the roots which grow in the dark and cannot directly transform light into chemical energy. Further, the stored energy can be employed at times when the sun's energy is not available, *e.g.* at night.

In intramolecular respiration also energy is set free; this does not, however, suffice in most organisms to maintain the driving force for the normal vital processes. Some seeds can remain alive for many hours or days with intramolecular respiration, and some even continue to give off the same amount of carbon dioxide as in ordinary respiration. In most cases, however, the amount of CO_2 rapidly diminishes. In other plants death soon occurs, probably owing to the end-products of intramolecular respiration acting as poisons. The value of intramolecular respiration is in these cases only slight. On the other hand it has a very great importance in certain organisms which will be referred to later.

B. OXIDATION OF INORGANIC MATERIAL (^{69})

While most plants use organic compounds, especially carbohydrates, in respiration, certain bacteria utilise other sources of energy. Thus, the nitrite bacteria which commonly occur in the soil oxidise ammonia to nitrous acid, and the associated nitrate bacteria further oxidise the nitrous acid to nitric acid (nitrification). By the help of the energy thus obtained they can then assimilate carbon dioxide; the chemical energy takes the place in them of the sun's energy for the typical autotrophic plant. The formation of the organic substance is, in this case, not a photosynthesis but a chemosynthesis. There is no breaking down of organic material so that the whole of the assimilated nutritive substance is retained, and the working of these organisms is very economical. Since, however, only a limited amount of ammonia is available, and this is derived from other organisms, they cannot take the dominant place in nature which the green plants do.

With the nitro-bacteria the so-called sulphur bacteria may be associated; these oxidise sulphuretted hydrogen to sulphuric acid, sulphur being an intermediate product, and being stored in the body of the plant. In a similar way other bacteria obtain energy by the oxidation of methane to carbon dioxide and water. It is very probable that the energy in these cases is employed in the synthesis of organic substances from CO_2.

In contrast to these strictly specialised autotrophic bacteria the combustion of hydrogen is not a property of definite "hydrogen-bacteria" but is widespread among ordinary heterotrophic bacteria; these further effect the oxidation of organic substances. The case is apparently similar for the so-called iron-bacteria (*e.g. Leptothrix ochracea*); these perhaps only require iron or manganese when supplied with unsuitable organic substances.

C. FERMENTATION (^{70})

With the removal of oxygen intramolecular respiration begins, but this cannot supply the necessary energy to maintain life in the higher plants, although it may do so in lower organisms. Many Bacteria, Fungi, and certain Algae (Characeae) are notably independent of a supply of oxygen; they succeed with slight traces of this gas, or they avoid it altogether and live in situations where oxygen is absent (mud of swamps or of the sea, digestive canal of many animals so far as it is free from oxygen). Such organisms are called anaerobes or

ANAEROBIONTS in contrast to the typical aerobes or AEROBIONTS. All intermediate stages connect the two extremes. The true anaerobionts decompose large amounts of organic substances, and this decomposition, which is in principle the same as the process of intramolecular respiration, is termed FERMENTATION. As in intramolecular respiration, these processes are concerned with obtaining combined oxygen.

The prototype of fermentation is the alcoholic fermentation brought about by the yeast fungus (cf. p. 443). In this, sugar is split up into alcohol and carbon dioxide, and the process has great technical importance in the production of beer, wine, and brandy. The chemical process is the same as that of intramolecular respiration in a green plant; in contrast to this the yeast plant obtains in the fermentation a complete substitute for respiratory activity. It is, however, only independent of oxygen when it is supplied with a suitable fermentable material (sugar). In the absence of sugar, oxygen is indispensable, and normal respiration takes place. When both sugar and oxygen are supplied, respiration and fermentation go on simultaneously; part of the sugar is transformed into C_2H_6O and CO_2 and another part into H_2O and CO_2. Obviously, the transformation of sugar into alcohol and carbon dioxide will provide much less energy than the complete combustion to carbon dioxide and water. It is thus easy to understand that yeast utilises enormous quantities of sugar. Only about 2 per cent of the sugar in the nutrient solution is used in the construction of the substance of the plant, *i.e.* is assimilated; the rest is fermented. For effecting this extensive decomposition of the sugar, yeast employs a specific enzyme (zymase).

While in normal respiration, the total heat of combustion of glucose (=674,000 gramme calories) is set free, there has to be subtracted in the case of alcoholic fermentation the heat of combustion of two molecules of ethyl alcohol (2 × 323,000 =646,000 gramme calories); thus only 28,000 instead of 674,000 gramme calories are set free.

It was long suspected that the fermentative power of yeast was dependent on the presence of enzymes (71). E. BUCHNER first succeeded in separating these from the living protoplasm. Since "zymase", in contrast to other enzymes, is unable to diffuse from the cells, these have to be ruptured and then subjected to great pressure to obtain it. Further, zymase is not a simple enzyme but a mixture of a number of enzymes which in conjunction bring about the alcoholic fermentation.

According to NEUBERG (72), in this process the molecule of sugar is first transformed into two molecules of methyl-glyoxal which provide pyruvic acid and glycerol; by the splitting off of CO_2 this is transformed into acetaldehyde. Acetaldehyde can be demonstrated as an intermediate product in the process of fermentation, and is also directly reduced to alcohol by yeast.

While the yeast fungus is largely unaffected by oxygen in its fermentative activities it cannot be classed with strictly anaerobic organisms, since its growth is greatly favoured by free oxygen. It follows from this, since the chemical changes depend on the numbers of the yeast cells, that more alcohol can ultimately be obtained in the presence of oxygen than if this is excluded.

Other fermentative organisms, however, are directly injured by free oxygen and therefore only occur naturally in situations where this gas is absent. To these true anaerobes the butyric acid bacteria belong; these transform all kinds of carbohydrates and higher alcohols into hydrogen and organic acids, butyric acid being always among the latter. Since they can attack cellulose, butyric acid bacteria play an important part in nature. They transform the carbon fixed in the cell-walls of plants into forms which other organisms can utilise; they thus prevent a large amount of carbon being excluded from the circulation of materials in nature (see below).

In the butyric acid fermentation also the carbohydrate is first transformed into pyruvic acid and glycerol; from this, butyric acid and free hydrogen arise. Since free nitrogen can act as an acceptor of the hydrogen, there is a formation of ammonia and thus a fixation of nitrogen.

It is impossible to treat of all the various fermentations here. The lactic acid fermentation may, however, be mentioned. This plays an important part in the dairy industry, and also in the preparation of Saüerkraut. The process is anaerobic, the molecule of sugar either splitting into two molecules of lactic acid or yielding CO_2 and H_2 in addition to lactic acid.

So far only fermentations of carbohydrates have been considered, but the more complex organic compounds of the plant- and animal-body, and in particular the proteins, may also be fermented. In the latter case the process is termed PUTREFACATION when it takes place in the absence of oxygen, and DECAY when oxidation is possible. In nature aerobic bacteria occur first in the fermentation of albuminous substances, and these prepare the way for anaerobic forms, so that a sharp distinction between decay and putrefaction is impossible. In all cases the proteins are first hydrolytically dissociated with the production of the substances already mentioned, especially amino-acids. These are further changed, first by the separation of NH_2, and then more profoundly; ill-smelling substances such as sulphuretted hydrogen, indol, and skatol are often, but not in all cases of proteid fermentation, formed.

It is impossible to draw a sharp line between those decompositions which go on without the assistance of atmospheric oxygen and those in which oxygen plays a part. We are obliged to class as fermentations all those metabolic processes by which energy is obtained, which differ from typical oxygen respiration. In this sense the production of malic and oxalic acids in the Crassulaceae and of oxalic acid in fungi and bacteria would be fermentations and a typical oxidation process (the transformation of alcohol to acetic acid effected by the acetic acid bacteria), must also be grouped with fermentations.

With these processes, which have in common a gain of oxygen, free or combined, there must lastly be associated the cases in which inorganic compounds serve as the source of the oxygen. Thus certain bacteria live as anaerobes using nitrates as their source of oxygen; the nitrates are reduced to free nitrogen (denitrification). In other cases sulphates are reduced to sulphuretted hydrogen.

There are further bacteria (*Micrococcus selenicus*) which are not anaerobic but are unable to utilise the free oxygen; they can only take oxygen from readily reduced substances such as sodium selinite, sodium thiosulphate, indigo carmine, or methylene blue (73).

Circulation of Material.—When organic material, as is the case in nature with the remains of dead organisms, is the prey of various micro-organisms these co-operate in their action; metabolic products of one kind of micro-organism are further decomposed by others until the organic compounds are converted into inorganic or mineral substances. The final products are carbonic acid, water, hydrogen, methane, ammonia, nitrogen, and sulphuretted hydrogen.

All these end-products of fermentation can be utilised by other organisms. Leaving CO_2 and H_2O aside as having been sufficiently dealt with, it may be noted that hydrogen, methane, ammonia, and sulphuretted hydrogen are all oxidised by particular bacteria, while others assimilate nitrogen. It is only by this co-operation of all organisms that life is maintained on the earth and substances again brought into circulation. If only one type of organism existed, it would in a short time have destroyed the possibility of its own existence by its one-sided metabolism.

D. PRODUCTION OF HEAT AND LIGHT IN RESPIRATION AND FERMENTATION

Heat (74).—Since typical respiration is a process of oxidation, it is easy to understand that it is accompanied by an evolution of heat. That this evolution of heat by plants is usually not perceptible is due to the fact that it is not sufficiently great, and that considerable quantities of heat are rendered latent by transpiration, so that transpiring plants are usually even cooler than their environment. In some fermentations, *e.g.* alcoholic fermentation, a considerable quantity of heat is evolved. The heat of rotting manure is well known and employed in the construction of hot-beds.

The spontaneous evolution of heat is easily shown experimentally, if transpiration and the loss of heat by radiation are prevented and vigorously-respiring plants are selected. A quantity of germinating seeds (peas) shows under proper conditions a rise in temperature of 2° C. The greatest spontaneous evolution of heat manifested by plants has been observed in the inflorescences of the Araceae, in which the temperature was increased by energetic respiration 10°-20° C. Also in the large flower of the *Victoria regia* temperature variations of 15° C. have been shown to be due to respiration. One gramme of the spadix of an Aroid exhales, in one hour, up to 30 cubic centimetres CO_2; and half of the dry substance (all the reserve sugar and starch) may be consumed in a few hours as the result of such vigorous respiration. Specially high temperatures are obtained by cutting up living leaves, etc., in large quantity and ensuring a sufficient supply of oxygen. Under these conditions the temperature rises to 40°-50° C., and the leaves perish. After their death a further rise of temperature is due to the action of micro-organisms.

On wounding plants, respiration and also the production of heat are markedly increased; the contrary is seen in conditions of starvation.

In the fermentation of tobacco also a considerable rise in temperature takes place. This is still more marked when damp hay or cotton wool is piled up in large quantity and left undisturbed; by the formation of easily inflammable gases, this may lead to the spontaneous combustion of the material. The spontaneous heating of hay has been most thoroughly studied. First by the respiratory activity of *Bacillus coli* the temperature is raised to 40° C.; then a number of thermophilous moulds and bacteria become established, among which *Bacillus calfactor* raises the temperature to 70° C. Ultimately all the organisms perish owing to the temperature to which they have given rise.

Phosphorescence (75).—Under the same conditions as those of respiration a limited number of plants, particularly fungi and bacteria, emit a phosphorescent light. The best-known phosphorescent plants are certain forms of bacteria which occur in the sea, and the mycelium, formerly described as "Rhizomorpha," of the fungus *Armillaria mellea.* Harmless phosphorescent Bacteria (*Bacterium phosphoreum, Pseudomonas lucifera*) occur on phosphorescent fish or meat. The phosphorescence of many animals appears usually to depend on bacteria which develop regularly in particular organs of the animals.

This phosphorescence disappears in an atmosphere devoid of oxygen, only to reappear on the admission of free oxygen. On this account the phosphorescent bacteria afford a delicate test for the activity of assimilation. All the circumstances which facilitate respiration intensify phosphorescence; the converse of this is also true. No use is known for the phenomenon of phosphorescence.

SECTION II

DEVELOPMENT (76)

DEVELOPMENT, that is, growth combined with change of form, is one of the most striking vital phenomena. A plant, composed it may be of millions of cells, commenced its existence as a single microscopically small cell; in order to attain its large size and definitive form it has had to develop. Developmental physiology does not see in the development merely the stream of changes in the construction of the organism shown by the developmental history regarded from a phylogenetic standpoint; it sees in the individual organism a series of successive, causally determined processes occurring as phases of development and bringing about the differentiation of the germ. The physiology of development has to recognise the special nature of each of these processes and to trace them to their underlying causes.

I. The Commencement of Growth (77)

The germination of seeds and spores.—The natural starting-point in considering the development of an individual plant is the germination of the seed in the case of the higher plants, and in the lower plants the germination of the spore. Ripe seeds or spores usually undergo a resting period which may be determined by internal or external causes. They pass into the so called latent condition in which all the manifestations of life come to an almost complete standstill; even respiration is suspended and there are no indications of growth or movement. When this condition is overcome the development commences with germination, that is, the formation of a young plant or seedling.

The germination of seeds and spores is brought about as a rule by the re-establishment of the general conditions for growth, especially a suitable temperature, supply of oxygen and water. In other cases this does not suffice; the resting state is dependent on certain internal conditions and often requires special stimuli to bring about a change.

Some seeds pass through a prolonged resting period before they commence to germinate. This may be due to the fact that they only become ripe after their separation from the plant, or it may be due to their only being able to absorb water very slowly. There are also great individual differences among seeds; some may lie for years in the soil, while others of the same age have germinated long before; this in part depends on the hardness of the seed-coat and the consequent difficulty of swelling. This also appears to be the main reason why the seeds of many aquatic plants (78) will not germinate in pure water, but do so on the addition of acids or alkalies. In some cases fully swollen seeds are unable to germinate except in the LIGHT (79). A surprisingly short exposure to illumination may suffice (*Lythrum salicaria*, $\frac{1}{10}$ second, at Hefner candle intensity of illumination 370). When the germination of seeds is tested in light of different wave-lengths, if the energy for all colours is equal the number of germinations is found to be proportional to the wave-length, thus the yield in germination can be represented as proportional to the number of light-quanta. Not uncommonly the illumination may be replaced by a particular high temperature or by the chemical effects of the light. Chemical stimuli play the chief part in the case of certain parasites which only germinate in the vicinity of their host plants (*Orobanche*, *Tozzia*). In other cases (*e.g.* *Amarantus*) light hinders or delays germination, and darkness is an advantage.

In the case of spores also, germination may begin on the establishment of the formal conditions of growth or may require special stimuli.

The unfolding of buds.—Unlike the animal the plant is never fully grown. It forms, as a rule in the leaf-axils, buds which undergo a period of rest and sooner or later unfold. The remarks made regarding the germination of seeds apply to the annual recurrence of the active growth of buds in perennial plants.

A striking and fixed resting condition is seen in deciduous trees. At a certain season of the year, in the autumn or earlier, their buds can in no way be induced to expand (stage of complete rest). Later, however, a considerable shortening of their resting period may be caused not only by a higher temperature but by a number of stimuli such as frost, dryness, darkness, illumination, ether vapour, acetylene, tobacco smoke, wounding, injection of water, etc. The awakening from the resting state (80) is most readily effected shortly before the normal resumption of activity, but almost as readily at an early period shortly after the period of rest has begun. These relations have to be taken into consideration in the forcing of plants in horticultural practice.

II. General Phenomena of Growth

When seeds or spores commence to germinate, or buds to unfold, growth begins. To be able to grow is a specific property of living structures, which is lacking in dead bodies. The "growth" of a crystal is something quite different. In it particles are removed from the surrounding liquid and applied to those that form the existing crystal, while with the process of growth are connected manifold movements of material in the living organism. In the latter case the result is not a simple enlargement resulting according to definite laws, but an increase of volume with which a host of very complicated internal changes are connected. Owing to this the increase of size is permanent and persistent and is irreversible. Thus an increase of size due to imbibition, as in the case of a dry seed placed in water, is not growth. Usually growth is associated with gain of material, but in the case of potatoes sprouting in a dark cellar loss takes place by transpiration and respiration, and yet the shoots exhibit growth.

1. The Phases of Growth

In the simplest plants, such as the lower Algae, Fungi, or Bacteria, development consists merely in growth of the cell followed by cell-division. These cases have been sufficiently dealt with in the morphological section. In more complex plants growth and division of cells are also found, but these processes appear subordinated to the growth of the whole. Three distinct processes can be distinguished in this, though they are not always separated in time. These are the stages of FORMATION OF EMBRYONIC ORGANS, of ELONGATION, and of INTERNAL DEVELOPMENT.

(a) Embryonic Rudiments.—The embryonic growth takes place normally at the **growing points.** Little is known as to the causes of the cell-divisions in the growing point. There is no doubt that a very complex succession of phenomena is involved; not only the protoplasm but the nuclei of the cells have to be considered, the latter indeed initiating the cell divisions.

In the first place there is no doubt that external factors play a great part in starting cell-divisions (81). It will be seen below (p. 286) that the intensity and quality of the light sometimes, as in fern prothalli, exert a great influence on the cell-division. In the second place internal factors, especially the age of the cells, come into play; the capacity for division diminishes with the age of the cells, but can be restored by external influences. As HABERLANDT (82) has shown, certain substances (hormones), which can thus restart the process of division, are derived from wounded or mechanically injured cells. Similar substances appear to arise in plasmolysis, perhaps by rupture of threads of protoplasm, and some poisons have a similar effect.

(b) Elongation.—The meristematic primordia require to enlarge and unfold before they can become functional, and this increase of size is effected in a peculiar and economical fashion. It results mainly from absorption of water from without. Organic material is of course required for the extension of surface of the cell-walls, but there is no need of an increase in protoplasm during the enlargement; the valuable nitrogenous material is economised. There is a great difference in this respect between the growth of a plant and a typical animal; nothing corresponding to this "phase of elongation" is met with in the latter.

The meristematic cells of the growing point contain considerable amounts of imbibed water in the wall and protoplasm. As absorption of water from without continues, a distinction becomes evident between the fully-saturated protoplasm and the vacuoles filled with a watery solution; this leads ultimately to the single large central vacuole or sap-cavity surrounded by the peripheral layer or sac of protoplasm (cf. p. 2, Fig. 3).

Since the elongation consists in an absorption of water it is evident that the cells which grow most strongly are those that have the greatest suction-force values. According to recent investigations, however, the turgor-pressure, to which importance was earlier attributed in connection with growth, plays a subordinate rôle. It has been shown by measurements that it diminishes in the growing zone in proportion to the growth (83). This diminution is very advantageous to the growing cell; since the suction-force, which is so important for growth, is equal to the difference between the concentration of the cell-contents and the pressure of the wall, the plant only requires to keep the former value constant in order to arrive at a greater value of the suction-force. Any serious dilution of the cell-sap need not occur owing to the power of the growing cell to regulate the concentration of the cell-sap. The osmotic value can be increased by the transformation of sugar into organic salts; thus, for example, by a change of glucose into oxalic acid it can be trebled.

Regarding the processes in the growth of cell-walls which are termed apposition and intussusception, what is necessary has been stated on p. 33. In growth in surface due to plastic stretching without addition of material, followed by the addition of new layers to the wall, the stretching due to turgor appears as a natural preliminary to the growth In the case of growth by intussusception the turgor-pressure appears less necessary.

TISSUE TENSIONS.—The expansion of the cells in length and breadth does not always take place uniformly and simultaneously in the whole cross-section of an organ. It is usual to find that, in growing stems for instance, the pith strives to expand more strongly than the peripheral tissues. Since no breach of continuity between the two regions is possible, a state of tension (tissue tension) results. The pith expands the cortical tissues and these compress the pith; the actual length of the organ is the resultant of these antagonistic tendencies. If the tissues are artificially separated, each assumes its own specific length; the pith elongates and the cortex contracts and the tension disappears.

The tissue tensions which occur generally in growing organs may be demonstrated in this way. In a sunflower shoot the pith is separated for some distance from its connections to neighbouring tissues by means of a cork-borer. On withdrawing the cork-borer the cylinder of pith projects for some distance from the cut surface of the stem (Fig. 252, *1*). If a similar shoot is split longitudinally the two halves curve outwards owing to the elongation of the pith and the contraction of the epidermis. Even in the case of hollow shoots such as the stalk of the inflorescence of the Dandelion (*Taraxacum*) a tension exists between the outer and inner tissues which is expressed by curvatures when the stalk is split longitudinally (Fig. 252, *2a*). If the stalk after this treatment is placed in water the curvature increases considerably (Fig. 252, *2b*).

Tissue tensions also occur in leaves and roots. The tensions need not be in the longitudinal direction alone; there are also transverse tensions. Thus, for example, the rind of trees which increase in thickness by secondary growth is considerably stretched in the tangential direction. On being separated from the wood it therefore contracts.

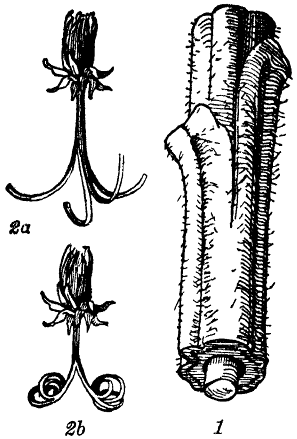


Fig. 252.—*1*, Shoot of *Helianthus annuus* with the leaves removed and the pith separated from the peripheral tissues by means of a cork-borer. *2*, Stalk of the inflorescence of *Taraxacum*, split longitudinally by two incisions at right angles to one another; *a*, just after splitting; *b*, after immersion in water.

The tissue tensions gradually arise at some little distance from the growing point where the expansion of cells is commencing, and as a rule they again disappear in the fully-grown zone, though they persist in the case of some organs (p. 339). They are of great importance for the rigidity of growing tissues; they increase the rigidity given by the turgescence of the individual cells. The tissue tension presents a certain resemblance to the turgescence of the cell; this is most evident in the typical stem. Just as the cell-sap distends the cell-wall by its osmotic pressure, the expanding pith stretches the cortical tissues.

The tissue tension ceases as all the cells attain the permanent mean length dictated by the size of the organ. Sometimes, however, certain cells after attaining their greatest length exhibit a considerable contraction associated with an alteration in shape. This occurs often in roots when the tissues of the cortex and of the central portion are thrown into folds by the contraction of the tissue that lies between them. The significance of this contraction of roots (p. 170), which may lead to a shortening of the fully-grown structure by 10-70 per cent, is very great. Thus it is due to it that the leaves of many "rosette plants," in spite of the continued growth in length of the stem, remain always appressed to the soil. It determines and regulates the penetration of many tubers and bulbs to a definite depth in the soil. It increases the fixation of the plant in the soil, since greater stability results from tense than from slack roots.

(c) Internal Differentiation.—The cells of the typical growing point maintain their power of growth and division. A portion of the meristematic tissue, or the whole of it in the case of organs of limited growth, becomes transformed into the somatic cells of the permanent tissues; in these growth and cell-division cease, and sooner or later death ensues (p. 308).

The internal development of an organ commences close behind the growing point and lasts for a longer or shorter time. While the full development of hairs is frequently very rapid, the definite form and structure of the internal tissues is often only completed after the phase of elongation is ended.

2. Measurement of Growth

Embryonic Growth.—The increase of size due to embryonic growth is too small to be easily recognised. It can only be established, noting the number of cell-divisions, by microscopical examination.

Such investigations have shown that there is an underlying rhythm in embryonic growth and that, even when the external conditions remain constant, it is not the same at all periods of the day. The various organs behave differently. Thus the maximum for roots is between 9 and 11 A.M., and for shoots 3-5 A.M. It has long been known that in many Algae, *e.g. Spirogyra*, cell-division occurs only at night (84). While in this case it is evident that light is the arresting cause, in the embryonic growth of higher plants still unknown external factors or internal causes are presumably acting.

Elongation.—It is usually growth by elongation that is in question when the growing parts of plants are considered and the growth measured.

(a) Total Elongation.—The rate of growth of a plant, or the total elongation in any unit of time, may be directly measured by means of a scale in the case of some quick-growing organs, *e.g.* the inflorescences of *Agave* and the shoots of *Bambusa.* Usually it is necessary to magnify in some way the actual elongation for more convenient observation. For large objects, the most convenient and usual method of determining the rate of growth is by means of an AUXANOMETER.

The principle of all auxanometers, however they may differ in construction, is the same, and is based upon the magnification of the rate of growth by means of a lever with a long and short arm. In Fig. 253, at the left, a simple form of auxanometer is shown. The thread fastened just below the terminal bud of the plant to be observed is passed over the movable pulley (*r*) and held taut by the weight (*g*), which should not be so heavy as to exert any strain on the plant. To the pulley there is attached a slender pointer (*z*), which is twenty times as long as the radius of the pulley, and this indicates on the scale (*S*) the rapidity of the growth magnified twenty-fold.

Self-registering auxanometers are also used, especially in making extended observations. In Fig. 253, at the right, is shown one of simple construction. The radius of the wheel (*R*) corresponds to the long arm, and the radius of the small wheel (*r*) to the short arm of the lever, in the preceding apparatus. Any movement of the wheel, induced by the elongation of the shoot, and the consequent descent of the weight (*g*), is recorded on the revolving drum (*C*) by the pointer attached to the weight *Z*, which is in turn balanced by the counter-weight (*W*). The drum is covered with smoked paper, and kept in rotation by the clockwork (*U*). If the drum is set so that it rotates on its axis once every hour, the perpendicular distances between the tracings on the drum will indicate the proportional hourly growth.

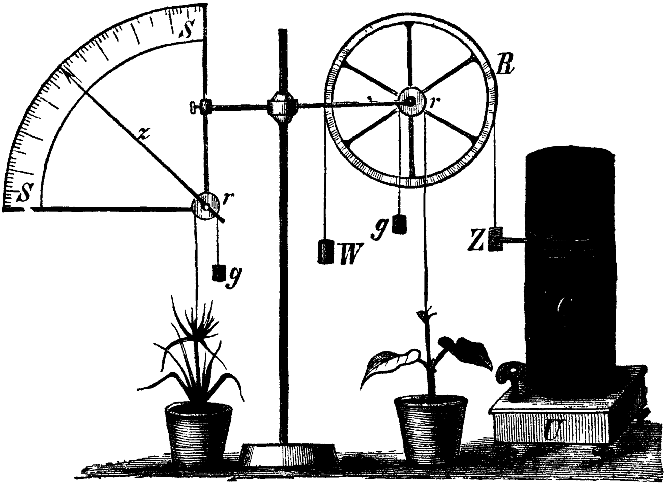


FIG. 253.—Simple and self-registering auxanometers. For description see text. (After NOLL.)

If more accurate measurements are required the horizontal microscope, focussed on the tip of the organ the growth of which is to be measured, may be employed. The growth is across a scale in the eye-piece and the space traversed by the growing tip can be magnified to any extent required. In order to obviate the constant readings a complicated self-regulating auxanometer has recently been constructed for these fine measurements (85). Cinematography has also been usefully employed in measurements of growth.

The rate of growth in plants is usually too slow to allow of the result being directly observed after a short time. Only some fungal hyphae and the stamens of some Gramineae grow so rapidly that their elongation is evident, even to the naked eye. The fructification of the Gasteromycetous fungus *Dictyophora* grows in length to the extent of 5 mm. per minute, and an increase in length of 1·8 mm. a minute has been observed in the stamens of *Triticum* (Wheat). This approximately corresponds to the rate of movement of the minute-hand of a watch. In comparison with these the next most rapidly-growing organ known is the leaf-sheath of the Banana, which shows an elongation of 1·1 mm., and a Bamboo shoot, with an increase in length of 0·75 mm. per minute; a strong shoot of *Cucurbita* grows 0·1 mm. per minute, the hyphae of *Botrytis* grow 0·034 mm., while most other plants, even under favourable circumstances, attain but a small rate of elongation (0·005 mm. and less per minute).

The rate of growth of an organ never remains uniform; even under constant external conditions it gradually increases from very small values to a maximum and then decreases to zero. This phenomenon is known as "the GRAND PERIOD OF GROWTH." An example will illustrate its course.

A coleoptile of the Oat cultivated at 22° C. in the dark gave the following measurements in millimetres at successive periods of 12 hours:

Half-days.	1.	2.	3.	4.	5.	6.	7.
Growth	3·7	14·3	22·3	24·0	12·7	4·7	0·8
Length attained . .	5·2	19·5	41·8	65·8	78·5	83·2	84·0

The figures for the increments of growth in the successive half-day periods, when plotted, give the black line curve in Fig. 254 which represents the grand period of growth. Instead of these numbers the second row of figures may be used to express graphically the course of growth. The dotted curve in Fig. 254 shows this for the values reduced to one-half; on account of its form this is termed the S-curve of growth.

The grand period is not always so regular as in this example; frequently deviations due to abrupt changes in the growth are apparent.

(b) Distribution of Growth.—As a rule any part of a plant is not growing throughout its whole extent but consists of both fully-grown and still growing portions. The latter also are not elongating uniformly but are composed of zones, passing gradually into one another, in which the rates of growth differ. The length and position of the growing zones is not the same in different organs. In typical roots the single growth-zone is situated near the tip and occupies a length of 5 to 10 mm. The growing zone is longer in aerial roots and in extreme cases may amount to 1 m. The behaviour of stems varies. Those without sharply-defined nodes have a single zone of growth of considerable length (frequently extending to ·5 m.). They thus resemble the aerial roots. In many shoots, especially those divided into nodes and internodes, there are a number of zones of growth separated by fully-grown or less strongly growing zones.

This is termed intercalary growth and is beautifully shown, for example, in the haulms of grasses, where a growing zone is found at the base of each internode. At the bases of many leaves also an intercalary growing zone is found.

The distribution of growth in any member of the plant is ascertained by periodically measuring the distance between certain natural or artificial marks.

Thus, for example, the tip of the root in Fig. 255 *I* is marked with lines of india-ink at intervals of 1 mm. The marks start from the growing point of the root (0) just behind the root-cap. Twenty-two hours later the marks had been separated from one another as is shown in Fig. 255 *II*. The elongation has been unequal in the different zones; at the upper and lower ends of the marked region it diminishes and thus leads to the fully-grown region on the one hand and the embryonal region at the tip on the other. Between these and nearer to the apical end is a zone where the maximal growth has taken place. If the growth of one transverse zone such as that between 0 and 1 is followed on successive days it is found that it grows at first slowly, then rapidly, and then again slowly. In other words, EVERY DIVISION OF THE GROWING ZONE EXHIBITS THE GRAND PERIOD OF GROWTH. The millimetre zones marked off from the apex are thus in different stages of their grand periods; the two first are on the ascending side of the curve, 3 and 4 are at the summit, and the others are on the descending slope of the curve. Other organs give corresponding results.

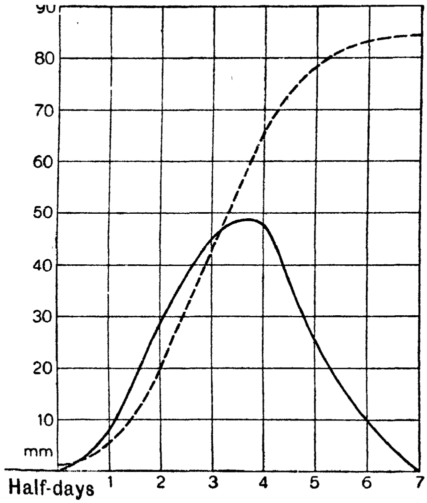


FIG. 254.—Curves of the course of growth. [Half-days.]

Distinct periods of growth separated by an interval of time occur in the scapes of the Dandelion, the first period in relation to the development of the flowers, the second to that of the fruits. A similar behaviour is found in other organs whose function after a time becomes altered (flower- or fruit-stalks in *Linaria cymbalaria*, *Tropaeolum*, and *Arachis hypogaea*).

(c) Rate of Growth.—From the fact that in different organs zones of different length are in a growing condition, it follows that such results as to the total growth of an organ as were described on p. 231 do not give the true rate of growth, *i.e.* the growth of a unit of length in unit time. Thus in the shoots of the Bamboo the growing zone is many centimetres long, while in *Botrytis* it is only 0·02 mm. in length. While *Bambusa* shows twice as much growth per minute as *Botrytis* does, its rate of growth is really much less. A certain relative measurement of the rapidity of growth is obtained by expressing the elongation per minute as a percentage of the growing zone. This gives a rapidity of growth of 83 per cent in *Botrytis*, and of only 1·27 per cent in *Bambusa*. The maximum growth observed is 220 per cent in some pollen-tubes, while some shoots which are still clearly growing have a rate of only 0·5 per cent.

(d) Size of the Plant.—We can only determine the definite elongation of a part of the plant when, in addition to the rate of growth and the length of the growing region, the duration of growth is known. The size of the plant, which, as is well known, depends in various ways on external conditions and yet is a specific character, is determined by variations in these factors. A definite size belongs to the specific properties of an organism just as much as the form of its leaves, etc.; further, the whole organisation of the plant is such that it involves a particular size.

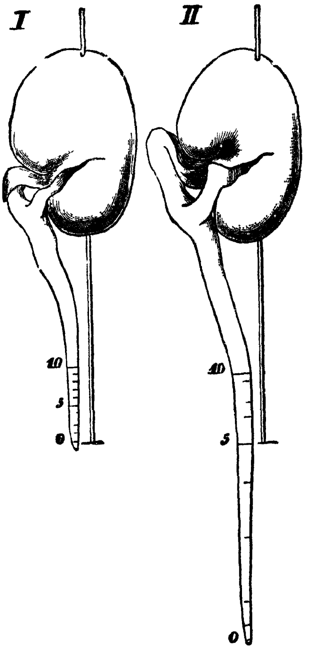


FIG. 255.—The distribution of growth in the root-tip of *Vicia Faba*. *I*, The root-tip divided by marking with india ink into 10 zones, each 1 mm long. *II*, The same root after twenty-two hours, by the unequal growth of the different zones the lines have become separated by unequal distances. (After SACHS.)

III. The Factors of Development

In attempting to determine the factors which influence development it is necessary to treat of examples which show in characteristic fashion the effect of particular factors. Completeness, either in the enumeration of the factors or as regards their influence, is out of the question. As in other cases, the factors may be divided into the two groups of external and internal factors.

A. External Factors

All the forces and substances which have been seen to be physiologically effective in the metabolism, or which play a part in movements, are among the external factors of development.

Certain external factors have already been mentioned (p. 203) as indispensable conditions of life; in the absence of these no development takes place. In addition to this general (formal) significance these factors have other effects on growth. On the one hand variation in the intensity of these factors usually calls forth definite quantitative changes in the course of growth, the so-called growth-reactions (cf. p. 305). On the other hand, modifications in the intensity, and also in the quality or the direction, of the factors may result in qualitative changes in the growing organs of the plant. These qualitative or formative influences find expression in two ways. They may be morphogenetic; influencing the resulting construction. They are further necessary to many organisms by determining the beginning of various phases of the developmental history, *e.g.* the commencement of development, the polarity, the general relations of symmetry, the cell-differentiation, the reproduction, etc.

1. **Temperature** (86).—As in the case of metabolism it is found that a certain temperature is a necessary formal condition of growth.

There is complete cessation of growth at a temperature less than 0° or higher than 40°-50° (cf. p. 203). Between the MINIMUM and MAXIMUM temperatures, at which growth ceases, there lies an OPTIMUM temperature at which the rate of growth is greatest (Fig. 256). This optimum temperature usually lies between 22° and 37° C. Plants inhabiting different climates exhibit considerable differences in regard to the cardinal points for temperature (cf. p. 204). The single individual of a particular species may make varying demands on the temperature during the successive stages of its development. Thus it may be impossible to regard any particular temperature as the optimum, without qualification. The seedlings of grasses, for example, succeed at temperatures which would seriously harm the plants when ready to flower. High temperatures which accelerate growth may, if prolonged, act injuriously on the development (cf. Fig. 256).

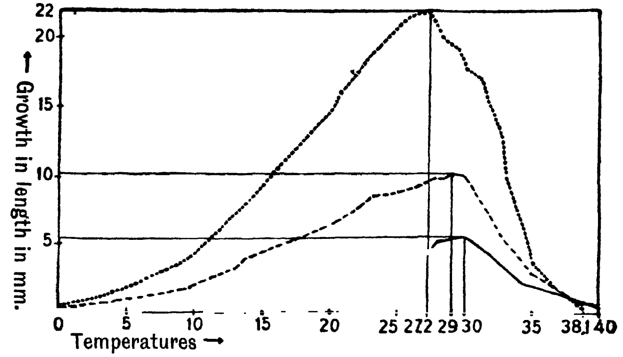


FIG. 256.—Dependence of growth on temperature. (After TALMA.) The abscissae give the temperatures. The curves give the growth of the roots of *Lepidium sativum*; the black line in 3½ hours; the broken line in 7 hours; and the dotted line in 14 hours. With the duration of the experiment the optimum shifts to lower temperatures.

In tropical plants the minimum temperature may be as high as +10° C., while those of higher latitudes, where the first plants of spring often penetrate a covering of snow, as well as those of the higher Alps and polar regions, grow vigorously at a temperature but little above zero. Many of our spring plants show that the opening of their flowers can take place at a lower temperature than the unfolding of the foliage leaves.

2. Light (^{87}).—Light is not so generally an indispensable condition of development as the temperature is. There are plants (Bacteria, Fungi) which can complete their whole development normally in darkness. On the other hand there are organs for which at least a transient illumination is necessary. It has been seen that certain seeds and spores only commence their development after they have had a short exposure to light. Plants which normally live in the light cannot continue their development unless they are exposed for periods to light. Light is indeed, as has been seen, essential for the construction of important materials for growth. Only those plants that are richly provided with reserve materials (seeds, rhizomes) are able to grow without light for longer periods. Even then they assume abnormal forms which have now to be considered (^{88}). If seeds of the White Mustard are sown in two pots, one of which is kept in the light and the other in darkness, the plants after a time exhibit the appearances represented in Fig. 257. The complete darkening has resulted in plants of a quite peculiar appearance. This phenomenon, which is known as ETIOLATION, comes about by the growth of some organs being unduly favoured and of others greatly retarded. The stems of Dicotyledons become unusually elongated, also soft and white in colour. The leaf-stalks are also lengthened, while the leaf-blades are small and remain for a long time folded in the bud (Fig. 257). Since in darkness the yellow pigments are formed but not the green pigments, the leaves of etiolated plants are yellow. Etiolation also occurs in some non-green plants; thus some cap fungi in the dark show considerable elongation of the stalk while the cap is abnormally small

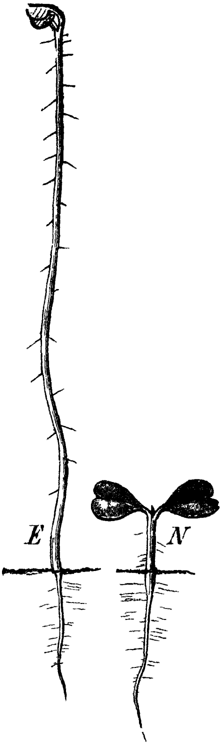


FIG 257.—Two seedlings of *Sinapis alba* of equal age. *E*, Grown in the dark, etiolated, *N*, grown in ordinary daylight, normal The roots bear root-hairs. (After NOLL.)

There are considerable differences in the anatomical structure between normal and etiolated plants. The tissues in the latter are little differentiated and thickened cells are wanting.

The elongation of certain organs and simultaneous reduction of others has an ecological significance in nature in the case of seedlings and rhizomes which are growing in the dark. The parts which are functional only in the light remain at first undeveloped, and the constructive material for them and especially for the chlorophyll is economised. The great elongation of the other organs, which is mainly dependent on an accumulation of water, brings the parts that need it as soon as possible into the light.

Comparison of an etiolated plant with one grown in the light shows that the influence of light is not the same on all organs; it may either increase or arrest the growth. While, however, the action of light in arresting the growth of the stem increases with the intensity, the increase of the growth of leaves due to the light has a limit; the leaf attains its maximal size in light of moderate intensity. It is a one-sided view of the growth in length of the stem, and the resulting height of the plant that is expressed by the statement, "the effect of illumination is to retard growth."

When the effect of various intensities of light on the growth of an organ is more accurately investigated it is found that an increase in the strength of the light does not at once arrest growth but exerts first a transient favouring influence. In a corresponding way a diminution in the intensity of the light first exerts an arresting influence and then the anticipated increase of growth takes place. The transient effects in both cases, however, do not influence the ultimate length; the organs grown in the stronger light are invariably smaller.

Even without going to the extreme of complete darkness, various intensities of illumination may have far reaching formative results. These are most accurately shown by the results of KLEBS' studies on fern prothalli. He found: 1. In weak light (osram lamp of 27 metre candles) the prothalli frequently form unbranched filaments, 2 mm. in length, but without any cell-divisions. 2. In somewhat stronger light the form of the young prothalli is the same, but transverse walls are formed. 3. In light of about 250 metre candles the filament is replaced by a flat expanse of cells; with the proper illumination even the second cell of the young prothallus can proceed to give rise to a cell-layer. 4. Lastly, in light of 500-1000 metre candles, small masses of cells are formed.

Further formative results from different intensities of light are shown in the form and structure of foliage leaves (cf. p. 107). Shade-leaves have a very different structure from the leaves of the same species developed in full sunlight. They are thinner, their palisade cells narrow below, leaving wide intercellular spaces between them, and form only a single layer; in sun-leaves the palisade cells are longer and form several layers.

Alpine plants, the illumination of which differs in duration, intensity, and composition from that in the plains, differ in their whole habit from lowland plants. Their vegetative organs are contracted, while the flowers are large and brightly coloured. Other factors than light are concerned in this change.

In cases where two types of leaf are produced in the course of development, as in *Campanula rotundifolia* and some water-plants, the juvenile leaves appear to be associated with weak light and the later type of leaf with light of a higher intensity (p. 306).

The effect of the various rays (89) of which white light is composed is not the same. It is especially the blue and violet rays of short wave-length that are effective when light arrests growth in length. The red rays, on the other hand, have the same effect as darkness.

In the case of fern-prothalli growth is favoured by red light as it is by darkness, but cell-division is arrested; on the other hand, the blue and violet rays arrest the growth but promote cell-divisions. Such differences in the effects of light are to some extent comprehensible when it is borne in mind that light acts not only as a stimulus but as a source of energy. Ultra-violet light has a harmful effect on the plant. Radium- and Röntgen-rays have an inhibitory effect on the processes of growth but, like poisons (p. 289), may in small amounts favour growth (90).

In addition to the intensity and quality of the light, its direction has a great effect on the form of the plant-body. One-sided illumination leads to curvatures (phototropism, cf. p. 350), but light has also an influence on the polarity (cf. p. 293) and symmetry of the plant. Thus, for example, a radial growing point may become bilateral or dorsiventral when illuminated from one side. Even an organ which has long passed the embryonic stage can thus become dorsiventral in so far as it only produces roots on the shaded side (shoots of Ivy and other root climbers). When the external symmetry has been altered experimentally the internal structure is also affected.

Antithamnion cruciatum, one of the Florideae, forms decussately-arranged branches when in diffused light; on one-sided illumination the branches all stand in one plane at right angles to the direction of the rays. Further examples of dorsiventrality induced by one-sided illumination are afforded by the branches of many Mosses, the thalli of most Liverworts, and the prothalli of Ferns; these structures in the absence of such illumination are sometimes radial and in other cases bilaterally symmetrical. In fern prothalli and the thallus of *Marchantia* the dorsal side is determined by the stronger illumination. In the case of the prothalli, when the lower side is illuminated, the new growth is adapted to the altered direction of the light and the former upper side becomes the lower; in the Marchantiaceous thallus, on the other hand, the dorsiventrality once induced cannot be changed.

3. **Gravity.**—A plant can readily be removed from the light but gravity is always acting upon it. It is only possible to change the direction of its action. When the direction of the action of gravity coincides with that of the main shoot and root of the plant no effect is perceptible; when it forms an angle with the line of these organs curvatures are produced (see Geotropism), as in the case of illumination from one side. Gravity can also, as in the case of light, transform radially-constructed into dorsiventral organs.

This is shown, for example, by the foliage buds of *Taxus baccata*, which only become dorsiventral under the one-sided action of gravity. The same holds for some zygomorphic flowers. Only under the one-sided orientating influence of gravity are the flowers of *Hemerocallis fulva* and *Epilobium augustifolium* dorsiventral; if the one-sidedness of the influence is removed the flowers become radial.

The formation of tissues may also exhibit a difference on the upper and lower sides of an organ that is due to gravity. A horizontally growing branch of a Conifer grows in thickness more strongly below than above and becomes excentric; this phenomenon is termed hypotrophy. The converse phenomenon, epitrophy, is often met with in Dicotyledonous trees (91).

4. **Mechanical Influences.**—Pressure and traction exert a purely mechanical influence upon growth, and also act as stimuli upon it. External pressure at first

retards the growth of the cell and ultimately arrests it. Since, however, the growth in surface of the cell-wall continues, the tension of the cell-wall ultimately disappears. When this process is complete the whole internal pressure of the cell is effective against the external resistance, and in many cases the osmotic value of the cell-sap is also increased. In this way roots may break open rocks. If the resistance of the body exerting the pressure cannot be overcome, the plasticity of the cell-walls renders possible a most intimate contact with it; thus, for instance, roots and root-hairs which penetrate a narrow cavity fill it so completely that they seem to have been poured into it in a fluid state. It would be natural to suppose that the effect of such a tractive force as a pull would accelerate growth in length by aiding and maintaining turgor expansion. But the regulative control exercised by the protoplasm over the processes of growth is such that the pull first acts as a stimulus upon growth to retard it, but then causes an acceleration of even 20 per cent.

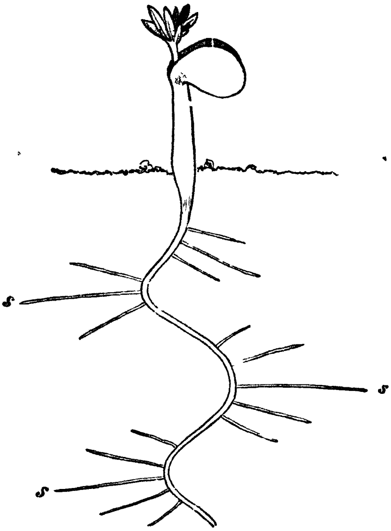


FIG. 258.—Young plant of Lupin, the main root of which has become curved. The lateral roots have arisen on the convex faces of the curves. (After NOLL.)

Other actions of mechanical influences as stimuli may be mentioned. Lateral roots arise only from the convex sides of curved roots (Fig. 258), the cause lying probably in the DIFFERENCES OF TENSION between the two sides. The primordia of the haustoria of *Cuscuta* and the adhesive discs on the tendrils of some species of *Parthenocissus* (Fig. 203) are caused to develop by the STIMULUS OF CONTACT.

5. Chemical Influences.—The presence of the necessary nutrient substances in sufficient quantity and the absence of poisonous substances are formal conditions for growth. While it is known that particular, essential, nutrient materials are not replaceable by an excess of others, some substances may be of special importance in particular processes. Since elongation is essentially due to the introduction of water, the significance of the water supply to a growing plant is obvious. Only the turgescent plant grows. Growth often ceases when there is not sufficient water in the soil. Dwarf plants (p. 161) often arise in dry soils (92). The water can often be taken from older parts, which then dry up while the tips of the shoots continue to grow, *e.g.* a potato sprouting in a cellar. Some plants can store water, and are therefore more independent of its direct absorption; they grow at the expense of the stored water.

The form and structure of plants may also be profoundly modified by the humidity of the air. When the atmosphere is damp the internodes and petioles tend to be long, the lamina large, thin, and with an entire margin; hairs are little developed and the differentiation of the tissues is not marked. There are thus in a number of respects similarities to etiolated plants. Local gorging of the tissues with water, as may result from the arrest of transpiration due to a coating of paraffin oil, leads to an increase in size of the cells and the formation of intumescences. In dry air, on the other hand, anatomical differentiation is well marked, the cuticle is strongly developed, collenchyma, sclerenchyma, and the vascular tissues are increased. There thus arise useful changes (adaptations) which have as a result the promotion of transpiration in moist air and its arrest under dry conditions.

A striking stimulus-effect results from permanent contact with liquid water in such plants as can endure this. This is doubtless the result of the combined effect of a number of factors and not simply due to the material effect of the water. Thus the arrest of transpiration, the change in the illumination, and the supply of oxygen are of importance.

Amphibious plants, that is such as are capable of living both upon land and in water, often assume in water an entirely different form from that which they possess in air. This variation of form is particularly manifested in the leaves, which, so long as they grow in water, are frequently linear and sessile or finely dissected, while in the air their leaf-blades are much broader and provided with petioles (cf. Fig. 135). The leaf-stalks and internodes also often exhibit a very different form in air and water, and undergo the same abnormal elongation as in darkness. This is especially noticeable in submerged water plants, whose organs must be brought to the surface of the water (stem of *Hippuris*, leaf-stalk of *Nymphaea*). Such plants are enabled by this power of elongating their stems or leaf-stalks to adapt themselves to the depth of the water, remaining short in shallow water and becoming very long in deep water.

The water-forms also differ from the land-forms in their internal structure. Thickened cell-walls are frequently absent from the stem, and the vascular bundles are reduced; the leaves resemble shade-leaves. The most marked contrast to water-plants is presented by such land-plants as are exposed to insufficient water supply or too active transpiration. In these the vascular bundles are strongly developed, while the epidermis has the arrangements which have been considered under the means of protection against excessive transpiration.

In addition to the true nutrient materials which are employed in the construction of the substance of the plant, oxygen requires to be mentioned. Although its entry into the plant is connected with a loss of organic substance, it is quite indispensable for growth on account of the need of respiration. In aerobic plants at least, growth ceases completely on the withdrawal of oxygen; a diminution or increase of the proportion of oxygen in the air also influences growth.

Stimuli of the most various kinds proceed from other substances acting on the plant (93).

Poisons must first be mentioned; these are substances which in very dilute solutions arrest growth and ultimately life. Thus even in a dilution of 1 in 100,000,000 copper sulphate kills such Algae as *Spirogyra* and also peas in water-cultures. It is a striking fact that many poisons when in extreme dilution have a stimulating effect on growth and determine a more efficient utilisation of other food materials. Chemical stimuli due to other substances play a large part in the germination of many seeds, spores, and pollen-grains, and in the development of fruits. Some pollen-grains only germinate when they obtain traces of substances which are present on the stigma. Many parasitic fungi and also parasitic Phanerogams (*Orobanche*, *Lathraea*) are stimulated to develop by unknown substances proceeding from their hosts.

6. Influence of Foreign Organisms.—Fungi and Bacteria living parasitically in flowering plants often cause profound deformations that are known as GALLS (94). In the simplest cases there is merely a hypertrophy of cells, while in more complex ones there are qualitative changes in the organ. Still more striking gall-formations are caused by animals, especially insects. Outgrowths form, which serve the parasites for protection and food. The structure of the gall appears purposive when considered from the side of the parasite, the protective layers and nutritive layers of the gall being without significance for the plant.

Euphorbia Cyparissias, when attacked by a rust fungus (*Aecidium Euphorbiae*), becomes sterile, remains unbranched, has shorter and broader leaves, and in its whole appearance is so changed as scarcely to be recognisable. Plant-lice sometimes cause a flower to turn green, so that instead of floral leaves green foliage-like leaves appear. Another peculiar example of abnormal growths is afforded by the GALLS or CECIDIA produced on plants by fungi, or more frequently by insects, worms, and arthropods. The effect of these formations on the normal development of the tissues of a plant is more or less disturbing, according to their position, whether it be in the embryonic substance of the growing point, in the tissues still in course of differentiation, or finally in those already developed. Galls which are products of abnormal tissue-formation are termed HISTOID, while ORGANOID galls depend on the transformation or new-formation of members of the plant body. The latter are especially instructive. The larvae of *Cecidomyia rosaria* live in the growing points of Willow stems, and occasion a malformation of the whole shoot by the production of galls, known as "willow-roses," which are composed of modified leaves and axes. Flies (Diptera) often deposit their eggs in the tissues of partially-developed leaves, in consequence of which the leaves become, according to their age when attacked, more or less swollen and twisted. After the leaves of the oak have attained their full growth they are often stung by a gall-wasp of the genus *Cynips*. The poison introduced by the sting, and also by the larvae hatched from the eggs deposited at the same time, occasions at first only a local swelling of the leaf tissue, which finally, however, results in the formation of yellow or red spherical galls on the lateral ribs on the under side of the leaf.

Symbionts (cf. p. 259 ff.) may influence one another formatively. This is seen, for example, in Lichens.

It is probable that, in addition to the wounding, chemical substances play an important part in the influences exerted by one organism on another. It is true that only in rare cases have deformations resembling galls been brought about by the action of dead substances extracted from the normal inhabitant of the gall. Parasites which do not give rise to galls probably act on the host plant by poisonous substances. On the other hand, the host plant by forming anti-bodies may injure the parasite or prevent its entrance. Thus HEINRICHER has shown that some kinds of pear-tree are readily infected by the mistletoe and others only with difficulty, he has also shown that probably one infection by the parasite renders the host more resistant to artificial infections. There are thus PHENOMENA OF IMMUNITY in the vegetable kingdom, though they have not been nearly so thoroughly investigated as in the case of animals (95).

7. **Survey of the External Factors**.—It has been seen that numerous external factors influence the plant; in the simpler cases they only affect the rate of growth, while in more complicated ones the influence extends to the resulting form. We tend to regard the form of a plant as usually met with in Nature as the NORMAL form. Deviations from this, that arise under the influence of external conditions, are spoken of as MODIFICATIONS of the normal form. It is clear, however, that the normal form itself is also the expression of definite external factors, those to which the plant is customarily exposed during its development. In other words, the same laws govern both the normal form and the modifications. The modification, like the constellation of conditions under which it appears, is unusual. While some of these changes in the plant are indifferent or even, as in the case of galls, are only of value to the organism giving rise to the alteration, many of the reactions of a plant to external stimuli are beneficial to the plant This is the case, for example, in the excessive elongation in etiolation, the characteristic construction of amphibious plants in water and on land, the protections against excessive transpirations in plants of dry habitats, etc. These are all useful reactions or ADAPTATIONS. Why the plant frequently reacts in this way cannot be further considered here (cf. p. 196). In contrast to such adaptations the modifications which are useless or injurious to the plant are termed MALFORMATIONS or pathological formations.

B. Internal Factors

When a change occurs in an organism while all the external factors remain constant it must be referred to internal factors. The latter cannot be so readily analysed as the external factors, so that the reference of phenomena to internal factors is frequently little more than a statement of our ignorance.

1. **Determinants.**—The determinants which a plant has derived from its parents are the first internal causes to be mentioned; it is these that lead to the regular origin of a particular fungus from a fungal spore or of a bean-plant from a bean-seed. In particular they determine the agreement of all the individuals of any species, when under the same external conditions, in such characters as the colour of the flower,

form of the leaf, size, etc. It is not as a rule possible to experimentally alter the determinants possessed by a species, and they cannot be ascertained by direct observation. Genetic experiments are needed to afford any insight into them. On this account further consideration of them may be deferred until heredity is treated later.

2. Form and Size of Cells and Cell-Division.—Since protoplasm is a liquid, the normal form of a naked cell is a sphere and this is often met with in unicellular organisms. Deviations from the spherical form are, however, frequent in these and become the rule when cells are associated to form a tissue. Mechanical pressure and tension and especially surface tensions give rise to profound alterations of the spherical shape. No causal mechanical explanation of the great variety of cell-form in plants is as yet possible, largely because so little is known of the important factor of the specific structure.

The theories bearing on the determination of the position of new walls in dividing cells are closely connected with the recognition of the fact that protoplasm is a tenacious fluid. It has long been observed that the position of the new cell-walls shows a striking similarity to the behaviour of weightless liquid films such as those of soap bubbles. The latter tend to contract to the least possible surface, and therefore are inserted as nearly as possible at right angles on the walls already present. In spite of the great similarity between the arrangement of cell-walls on the one hand and of surfaces of minimal area on the other, it would be unsafe to conclude that the same causes determine the position in the two cases, for the cell-wall is never fluid.

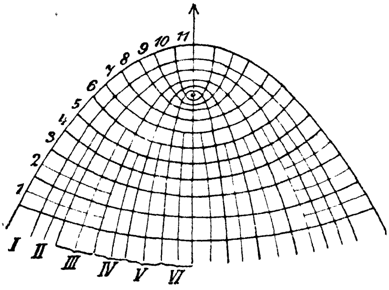


Fig. 259.—Diagrammatic representation of a growing point. (After Sachs.)

The principle of the rectangular intersection of cell-walls is strikingly shown in the growing points of phanerogamic plants. In these, as is shown in Sachs' diagram (Fig. 259), the cell-walls form two systems of parabolas which have a common focus and intersect at right angles. The one system (Fig. 259 *I-VI*) runs more or less parallel to the surface of the growing point; these cell-walls are termed PERICLINAL. The walls at right angles to these (1-11) are termed ANTICLINAL.

The growth of the cell once started does not always proceed uniformly. Some algal cells (*Vaucheria*) or fungal hyphae (*Saprolegnia*) continue to elongate by apical growth. In the great majority of cases, however, there is a limit to this, and when a certain size has been exceeded the normal mass of the cell is regained by cell-division.

Among higher plants also there are cells, such as the laticiferous tubes of the Euphorbiaceae which can continue to grow for years and attain a considerable length without undergoing cell-division. It is thus impossible to regard cell-division as necessarily following growth. What the factors may be that determine whether cell-division shall occur or not in particular cases is unknown; they belong to the group of numerous internal factors that determine development (96).

The size attained by cells must also be related to the internal conditions. If various species of plants are compared as regards the size of their cells it is found that a mean measurement is characteristic and is determined by heredity. Recent researches have disclosed the important fact that the nuclear mass contained in a cell has frequently a connection with the size of the latter It has proved possible in a number of cases to obtain cells with nuclear masses that are twice, four times or more that of the normal nucleus. In many cases all the cells derived from such a cell were considerably larger than normal and the increase in size appeared to be definitely connected with the condition of the nucleus (97a).

It was SACHS who first called attention to the great importance of the size of the cells for the organisation and construction of the plant. He pointed out that, in comparison with the enormous differences in size of different plants, the differences in size of cells were much less (97b). While, for example, the size of a bacterium and that of *Sequoia* are as 1 : 100,000,000, the ratio between the cell-sizes of the two organisms is only about 1 : 30. Plants of very different sizes are thus constructed of cells which differ much less in size than might have been anticipated.

3. **The structural organisation of the developing cells** may be of fundamental significance for the development. The egg from which the plant proceeds may be so constructed that all portions of its protoplasm are equivalent and that it possesses no definite structure to determine the typical development. On the other hand there may be already present in the egg-cell a definite organisation connected with the parts of the future plant. Which of these two possibilities holds for a particular plant can only be determined experimentally. For the egg of the sea-urchin, a favourable animal type for investigation, the first of the two alternatives stated above holds; the embryo can develop to a normal whole animal when parts of it have been detached. Something similar has been found in the early developmental stages of marine algae, *e.g.* Fucaceae. A decision on this point is hardly possible in the case of the higher plants in which the embryo, enclosed in the ovule, is not accessible to experimental interference. Further light on this group of questions can only be sought experimentally by investigations on restitution and polarity.

(a) **Polarity.**—By polarity is understood the property of the plant which determines the contrast between base and apex. In higher plants the polarity is already determined in the egg-cell and once established persists throughout the development. The fertilised egg proceeds to form two distinct growing-points one of which develops as the root and the other as the shoot of the embryo plant. A corresponding polar differentiation establishing base and apex is met with in simply constructed plants. In some cases an external factor determines which portion of the young plant will become the base and which the apex. Thus in the germination of the spores of *Equisetum*, the position of the first segment-walls, and thus the polarity, is determined by the direction of the incident light. A corresponding effect of light on polarity is shown by the eggs of *Fucus* and *Dictyota*. The influence of gravity on the polarity of plants has been frequently investigated. It has never been found possible, however, by inverting a plant to transform the shoot into a root and conversely. Even the polarity in the undifferentiated egg cannot be thus altered by gravity. It is evidently determined by internal causes, and gravity can only exert a modifying effect (98).

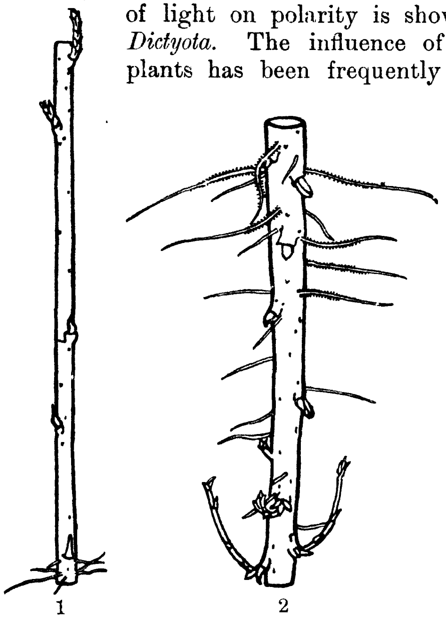


FIG. 260.—Twigs of Willow: 1, in the normal position; 2, in the inverted position growing in a moist chamber. (After VÖCHTING.)

While thus in some cases an external factor may determine which parts of a young plant shall become base and apex, in all the higher plants the polar growth is a specific character dependent on internal causes. It is as impossible to cause an apolar alga to exhibit polarity as to render a higher plant apolar or to invert its usual polarity.

If twigs of Willow are cut and suspended in a moist chamber roots form near to the lower end, while only the buds situated near the other end expand into shoots (Fig. 260, 1). If the twig is hung in the inverted position it is the corresponding buds at the end which is now lowest which still give rise to shoots, while the strongest roots are produced near to the lower end which is now uppermost (Fig. 260, 2). This experiment shows that internal causes mainly determine the contrast of the two poles. Since, however, in the inverted position there is a displacement downwards of root-formation and upwards of the unfolding of the buds gravity must also play a part. It has, however, in no case proved possible to effect a complete and lasting inversion of the polarity of a plant in this way; while such inverted plants may live for a considerable time, they exhibit serious disturbances in their anatomical construction (99). An effect of gravity on the internal disposition is also seen in the case of obliquely or horizontally placed branches. The tendency of the internal disposition is to cause the uppermost buds to develop and give rise to long shoots. On branches displaced from the vertical the basal buds are favoured and the more apical buds arrested. When the branch is curved the strongest branches arise at the highest point of the curve. In the cultivation of vines and fruit trees this peculiarity is utilised to produce shorter and weaker shoots (short shoots), which experience has shown are those that bear the flowers.

The polarity once it has been defined in the egg-cell is on the whole maintained throughout growth. In some plants, however, it can be seen to be altered from internal causes. Thus in species of *Platycerium* and *Adiantum* among the Ferns and in *Neottia nidus avis* among the Orchids, shoots are formed directly from the growing points of roots. In the Adder's-tongue Fern (*Ophioglossum*) the vegetative reproduction depends entirely on the formation of buds close to the growing points of the roots. The apices of some fern leaves also (*e.g. Adiantum Edgeworthii*) may grow directly into a shoot.

(b) Restitution (100).—The normal development with all its phases takes place even when the external factors remain completely constant. It is natural to enquire whether this is due to each part of the embryo bearing within it its future determination (theory of germinal districts); or whether, while the nucleus of the germ-cell contains the totality of the determinants for the whole organism, in the nuclear divisions of the embryo these determinants are distributed in a mosaic-like way to the resulting cells (theory of differential divisions)? In this case the mature cells of the various organs would only contain the particular determinants for the latter. Lastly, do all the cells of the body, like the germ-cell itself, possess the power of producing the entire organism? On questions like these the facts regarding restitution throw some light.

By restitution is understood the new-formation of organs which as a rule follows the mutilation of a plant, and can take place in situations where no active growth would have been manifested in an uninjured plant. Two types of restitution may be distinguished according to whether the new development occurs at the wounded surface or at some distance from this.

The production of the lost organ from the wounded surface, though not uncommon in lower plants such as algae and fungi, is of very restricted occurrence in the higher plants. Only tissues that are meristematic or embryonic, and by no means all of these, are capable of this. It is most frequently seen in the growing point of roots; when the tip is removed by a transverse cut, if this is not more than 0·5 mm. from the tip, it may be again formed. A longitudinally-split root-tip tends to complete itself in such a way as to give rise to two growing points. This type of restitution does not occur at the growing points of shoots, and is very rare in the case of leaf-primordia.

Another type of restitution, on the other hand, is widespread among plants. In this case an organ which has been lost is replaced either by the formation of a new one in the vicinity of the wound or the outgrowth of one which was in a rudimentary condition. Examples of this type of restitution are afforded by the algae and fungi, and especially by bryophyta. These can only be mentioned here, and consideration will be limited to the flowering plants. The capacity to form roots is especially widespread. In geraniums, willows, and many other plants, roots can be induced to form at any point on shoots separated from the plant. In other plants the roots develop at particular places such as the older nodes. After roots have developed, the stem gives rise to a complete plant either by the unfolding of axillary buds or by the development of new growing points of shoots. Separated leaves are often able to form roots, though the power of giving rise to a new shoot is rarely connected with this. Even separated roots, when they are able to give rise to buds, may regenerate new plants. Regenerative buds may also arise on tendrils, flowers, and fruits.

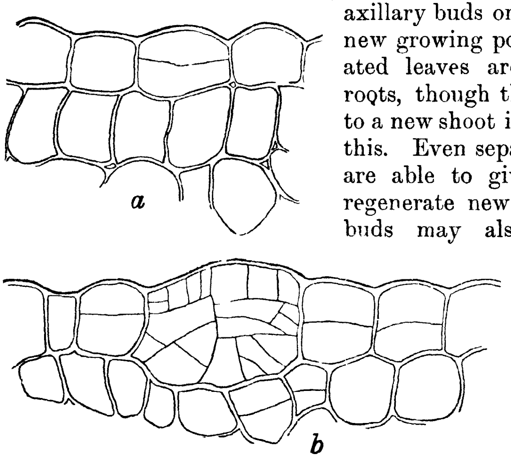


FIG. 261.—Transverse section of the leaf of *Begonia* showing the development of an adventitious shoot from an epidermal cell. *a*, The epidermal cell has divided once; *b*, a multicellular meristem has been produced. (× 200. After HANSEN.)

If the growing point of a flowering plant is destroyed a new growing point may be developed from the meristem above the youngest leaf-primordium. While the restitution is here restricted to meristematic cells, in other cases older fully-grown cells may recommence to grow and divide and thus return to the meristematic condition. A special tissue, called CALLUS, is thus first formed at the wounded surface, and new shoots may form within this. In yet other cases fully-grown epidermal or parenchymatous cells may give rise to growing points directly, *i.e.* without the formation of callus. Fig. 261 shows the origin of a shoot from an epidermal cell of a leaf of *Begonia*.

Tissues may also be regenerated from mature parenchymatous cells. Thus when the conducting tracts are interrupted new vessels may be formed from the parenchyma and re-establish the connection. The tissues which have been removed or interrupted are, however, not always formed anew; frequently substitutionary growth takes place. Thus, as a rule, an epidermis is replaced by cork, and it is exceptional for a true epidermis with stomata to be regenerated.

The new-formation of epidermis, which occurs in the normal course of development in certain Araceae with perforations in their leaves, may be referred to here. In *Monstera deliciosa* particular limited regions of the laminae of quite young leaves die. Around these spots the mesophyll divides and forms from the outermost layer of cells a secondary epidermis, clothing the perforations and connecting with the primary epidermis of the upper and lower surface of the leaf.

In addition to the fact that restitution occurs, the question as to where this takes place is of interest. The polarity which exists in the intact plant is frequently manifested in restitution. Thus shoots tend to appear at the apical end and roots at the basal end of portions of stems, while the opposite distribution is found in roots. In more lowly-organised plants polarity is often apparent in the restitution process, as when each of the single cells separated from a *Cladophora* forms a colourless rhizoid at the base and a green filament at the apical end.

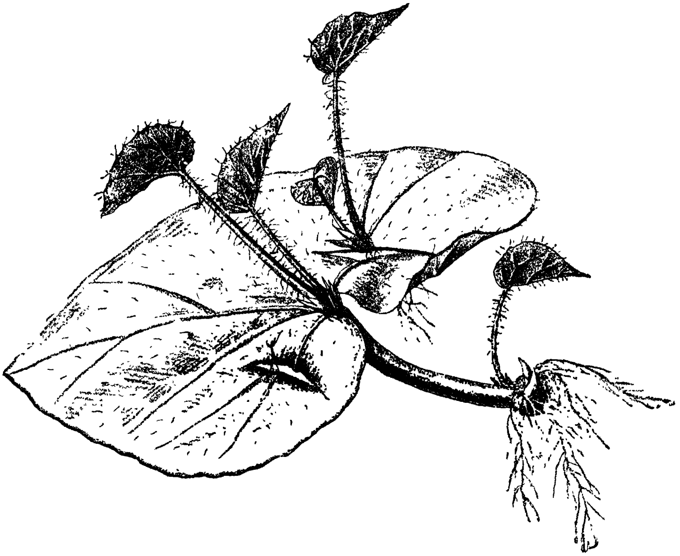


FIG. 262.—Leaf of *Begonia* used as a cutting and bearing restitution shoots. (After STOPPEL.)

This contrast of base and apex does not appear in restitutions from foliage leaves; this may be connected with the fact that the leaf is not included in the new formation. Frequently a new plant arises at the base of the leaf, which then dies off. Sometimes the new formations proceed from the general surface of the leaf (*Torenia*), but frequently the place of their origin can be determined by cutting the lamina, the new plants forming above the incisions (*Begonia*, Fig. 262) (^{101}).

The phenomena of restitution have great importance in horticulture, since they allow of plants being rapidly multiplied without the aid of seeds. In artificial reproduction detached pieces of plants are made use of for the purpose of producing fresh complete plants. In many cases this is easily done, but in others it is more difficult or even impossible. The simplest method is by means of CUTTINGS, that is, the planting of cut branches in water, sand, or earth, in which they take root (*Oleander*, *Pelargonium*, *Tradescantia*, *Fuchsia*, *Willow*, etc.). Many plants may be propagated from even a single leaf or portion of a leaf, as, for instance, is usually the case with Begonias. In other cases the leaves, while still on the parent-plant, have the power to produce adventitious buds (*Bryophyllum*). The Dandelion (*Taraxacum*) possesses the capability of developing from small portions of the root.

4. The Phenomena of Correlation (102).—The phenomena of restitution show that not only the cells of the embryo but even fully grown cells of the body of the plant are capable of reproducing the whole organism. The cells of a plant are thus TOTIPOTENT, resembling the germ-cells in this; and not UNIPOTENT. The most fundamental problem of developmental physiology is in what way the totipotent cells are induced to develop only a small proportion of their potentialities (or determinants). From every cell of a growing point the whole organism could develop. It is the mutual connections or correlations between the cells that lead to the lines of development followed by this and that cell. When these connections are removed it has been seen in the phenomena of restitution (p. 295) how cells exhibit quite other capacities than those they had previously shown when in connection with one another. This applies to mature as well as meristematic cells when their connection with neighbouring cells is interfered with. Thus it has been seen how fully grown cells that would soon have perished again become young, and how, for example, from a single epidermal cell all the various cells characteristic of the particular plant can be derived. It is clear that an organism in which such mutual action of the cells was lacking could not exhibit the division of labour that is customary in the higher plants. In other words correlations must be included among the "regulations" without which the organism is inconceivable.

Such correlations exist between the externally visible organs of a plant as well as between its cells. This, if not as a rule evident, becomes apparent when an organ is removed and the reactions of the isolated organ and of the plant from which it was taken are studied, or when an organ is experimentally brought into a position it did not previously occupy.

The first result of the removal of an organ may be the appearance of so-called COMPENSATIONS; other remaining organs become larger. The leaves which arise at the growing point prevent older leaves attaining their maximal size, and if the growing point is removed the size of the leaf may be increased (*e.g.* in the tobacco plant). The active development of some of the axillary buds hinders that of many others; if the dominant shoot is removed the resting buds commence to grow. The conclusion may be drawn that, even in normal development, the size of the organs is determined by correlative influences from neighbouring organs.

In other cases a QUALITATIVE effect follows the removal of an organ. If the tip of a Pine is removed, its place is taken by one of the adjacent lateral branches, which assumes the erect position and shows the same leaf-arrangement as the original main shoot. It appears that the usual oblique position and dorsiventral arrangement of the foliage on the lateral branches comes about under the influence of the main shoot. In this and many other cases of correlative influence it is not necessary that the organ should be removed; as a rule it is sufficient to interfere with its normal function, as for example, by embedding it in plaster of Paris.

As a further example of the mutual influence of the organs of a plant the formation of tubers in the Potato may be considered. As is represented in Fig. 196 the tubers usually form at the ends of horizontal stolons which arise from the lower region of the foliage shoot where it is embedded in the soil. The tuber forms by marked growth in thickness of the end of the stolon, and cessation of its growth in length. If, however, the leafy shoot is removed at the proper time, the ends of the stolons grow into erect branches which emerge from the soil and bear foliage leaves. The typical development of the Potato can thus be modified so that no tubers are formed. On the other hand, tubers can be caused to form at other places: for example, at low temperatures the main axis of a particular kind of Potato will remain short, and be transformed into a tuber; in other varieties tubers are produced near the summit of the aerial leafy shoots when the tip of the shoot is darkened. *Boussingaultia baselloides* is even more plastic than the Potato; any bud can be induced to form a tuber, and when buds are lacking, internodes or roots may swell into tubers. Apparently the production of a certain amount of reserve material acts as a stimulus leading to the formation of a storage organ.

It has been shown in considering restitution (p. 295) that new roots or shoots may be developed upon isolated organs. Thus, just as every cell is originally capable of assuming various forms, so are the members of the plant. It is only their mutual influence on one another that prevents this. It would be a mistake to think of such influences as only negative and leading to arrest of development. It is certain that one part of the plant may exert a positive determining influence on others. Thus it is extremely probable that growing buds determine the formation of conducting tracts in the underlying portions of the stem. As another example, the nucleus plays a certain part in the origin of the cell-wall.

The exact nature of such influences is unknown. Recent investigations support the assumption that they are often brought about by substances which can pass from a region where development is proceeding to other organs. Such substances which exercise a determining effect in the formative processes of plants are termed HORMONES. Their chemical nature is still completely obscure.

The effect of correlation is also shown when an organ is transplanted to a new position. By methods of transplantation, which have been derived from horticultural practice, it is easy in the case of many plants to make a separated part grow in relation to a wounded surface. The separated part is termed a graft, while the plant upon which it is inserted is called the stock. The graft may be of the same species as the stock, or from a related kind of plant. One correlative influence which is apparent is the suppression of restitution on the part both of the stock and the graft. The latter adopts the root-system of the stock, while the stock in turn adopts the shoot-system of the graft; there is no necessity for the formation of new organs.

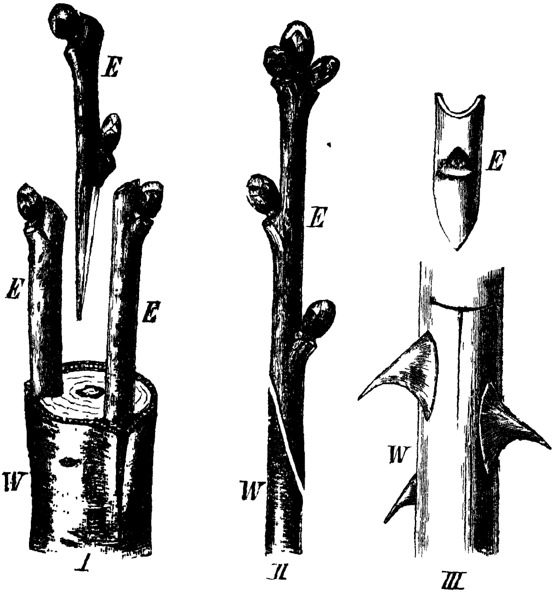


FIG. 263.—Different modes of grafting. *I*, Crown grafting, *II*, splice grafting, *III*, bud grafting; *W*, Stock; *E*, scion. (After NOLL.)

Artificial GRAFTING, like artificial propagation, plays an important part in horticulture. Separated shoots bearing buds serve as the grafts or scions, and are caused to unite with a rooted plant as the stock.

In practice several different methods of inserting grafts are in use, but only the more important can be mentioned here. GRAFTING is the union of a shoot bearing buds with a young and approximately equally-developed wild stock. Both are cut obliquely with a clean surface, placed together, and the junction protected from the entrance of water and fungi by means of grafting-wax (Fig. 263 *II*). Cleft or tongue grafting is the insertion of weaker shoots in a stronger stock. Several shoots are usually placed in the cut stem of the stock, care being taken that the cambial regions of the different portions are in contact, and that the cortex of the shoots is in contact with that of the stock. In other methods of grafting, the cut end of the shoot is split longitudinally and the cut shoot is inserted in the periphery, or a graft may be inserted in the cortex or in the side of the stock. In grafting in the cortex the flatly-cut shoot is inserted in the space cut between the bark and the splint wood (Fig. 263 *I*). In lateral grafting, the shoot, after being cut down, is wedged into a lateral incision in the stock.

A special kind of grafting is known as BUDDING (Fig. 263 *III*). In this process a bud ("eye") and not a twig is inserted under the bark of the stock. The "eye" is left attached to a shield-shaped piece of bark, which is easily separated from the wood when the plants contain sap. The bark of the stock is opened by a T-shaped cut, the "eye" inserted, and the whole tightly covered. Occasionally some of the wood may be detached with the shield-shaped piece of bark (budding with a woody shield). In the case of sprouting buds, the budding is made in spring; in dormant buds, which will sprout next year, in summer.

The union is accomplished by means of a callus (p. 296), formed by both the scion and the stock. Vessels and sieve-tubes afterwards develop in the callus, and so join together the similar elements of the two parts. Such an organic union is only possible between very nearly related plants: thus, for example, of the Amygdalaceae, the Plum, Peach, Almond, and Apricot may readily be grafted one upon the other; or of the Pomaceae, the Apple with the Quince; but not the Apple with the Plum, nor (as has been asserted) with the Oak.

The polarity which is noticeable in phenomena of restitution also influences the practice of grafting. Unlike poles of a plant may readily be induced to grow together, while like poles may only be brought to do so with difficulty, and then do not develop vigorously.

The stock and graft influence one another in a variety of ways. For example, portions of annual plants grafted on perennials attain an extended period of life; the opposite effect, a shortening of the life of the graft, may also result from grafting. Qualitative changes may also be brought about and may go so far as to lead to a vegetative bud of the graft becoming transformed into a flowering shoot. The specific properties of the two components are, however, maintained in cases of transplantation. Certain cases known as graft-hybrids (chimaeras) appear at first sight to constitute an exception to this statement; fuller investigation, however, shows that, while externally they appear intermediate formations between the symbionts in the graft, no mingling of the specific characters has taken place.

Chimaeras (^{103}).—Some plants grown in Botanic Gardens under the names *Laburnum Adami* and *Crataegomespilus* suggest in a number of ways comparison with hybrids (p. 314), but have undoubtedly not arisen by sexual reproduction. *Laburnum Adami* (Fig. 264) is intermediate between *Laburnum vulgare* and *Cytisus purpureus*; it frequently develops branches which can only be regarded as "reversions" to *Laburnum vulgare*, and less commonly others that completely resemble *Cytisus purpureus*. Certain intermediate forms between *Crataegus monogyna* and *Mespilus germanica* are known as *Crataegomespilus* or Bronveaux hybrids. The origin of these is known. The intermediate

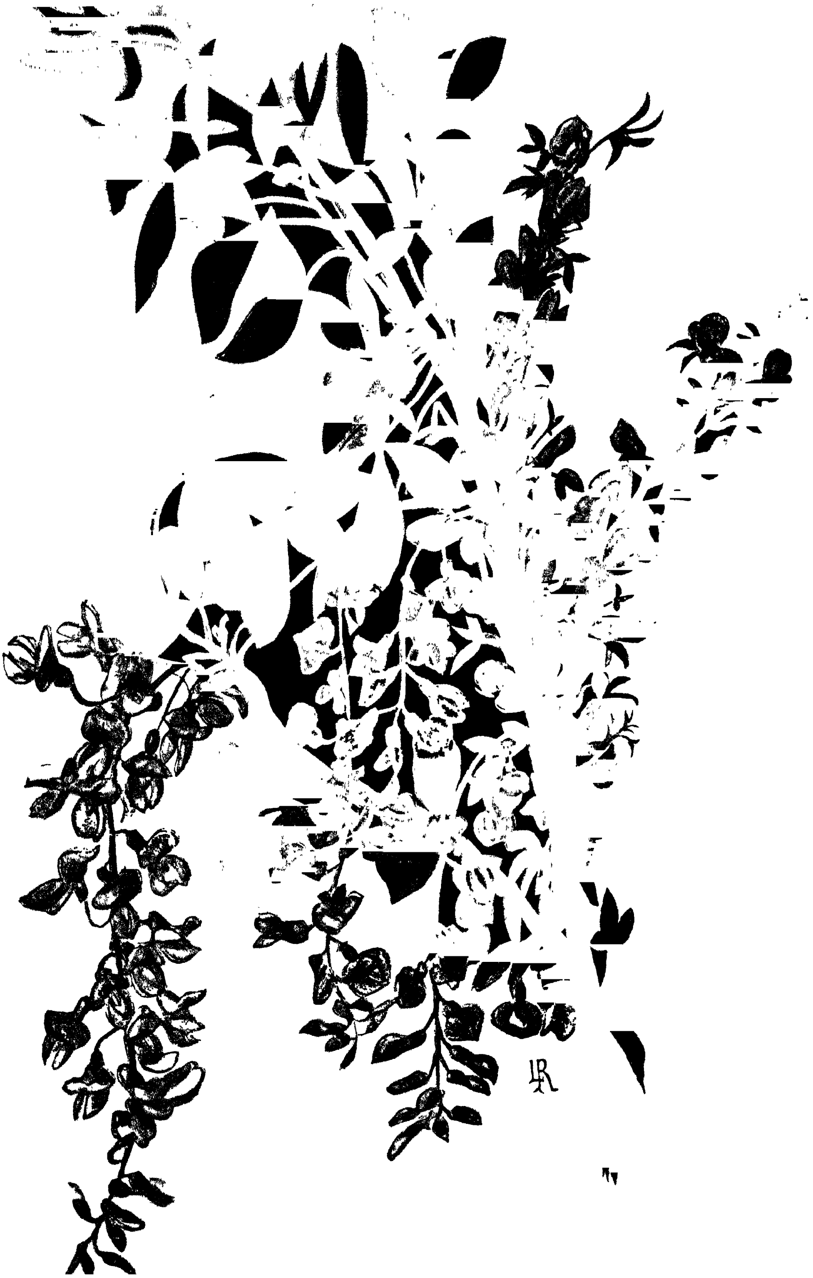


FIG 264.—*Laburnum Adami*, Poit (*Cytisus Adami*, Hort), with atavistic branches showing the characters of the two parental forms *Laburnum vulgare* to the left and *Cytisus purpureus* to the right (After NOLL.)

forms, of which several are known differing from one another, arose in the region of a graft of *Mespilus* on *Crataegus* in a garden at Bronveaux near Metz. It can be regarded as certain that the origin of *Laburnum Adami* was similar. Both plants have therefore been regarded as GRAFT HYBRIDS, *i.e.* as hybrids not resulting from the union of sexual cells, but by some influence of vegetative cells on one another.

More recently HANS WINKLER has produced such "graft hybrids" experimentally. He grafted *Solanum nigrum*, the Woody Nightshade, on *Solanum Lycopersicum*, the Tomato, and after union had taken place cut the stem of the stock transversely at the level of the graft. Among the adventitious shoots which developed from the region of junction of the two components there occurred well-marked intermediate forms. In the first instance there were forms which were composed of longitudinally-united halves with the characters of the grafted plants; these were termed chimaeras by WINKLER. Later there were obtained other intermediate forms, externally uniform (Fig. 265), which appeared to be the desired graft hybrids. Closer investigation showed, however, that these also were to be regarded as chimaeras, since they consisted of parts of the Tomato and the Nightshade intimately united in growth but otherwise unchanged. They were not longitudinally-united halves, however, but inner and outer layers of the growing point were formed of tissues of the two different species (cf. p. 82 and Fig. 265). These have therefore been termed PERICLINAL CHIMAERAS in contradistinction to the SECTORIAL CHIMAERAS in which longitudinal segments are evident.

Cytisus Adami and the *Crataegomespili* are also periclinal chimaeras. True graft hybrids in which a mingling of the specific characters in a single cell has resulted from grafting are as yet unknown.

Solanum tubingense has the dermatogen of the Tomato, while the internal tissues are those of the Nightshade. The converse is the case for *Solanum Kolreuterianum*. In *S. proteus* the two outer layers are from the Tomato and the remainder from the Nightshade, while *S. Gaertnerianum* affords the converse condition (Fig. 265). In a corresponding fashion the dermatogen in *Cytisus Adami* is derived from *Cytisus purpureus* and the internal tissues from *Laburnum vulgare*. In one of the Bronveaux hybrids (the form *Asnieresii*) a core of *Crataegus* is covered by the epidermis of *Mespilus*; the other form (*Dardari*) has two or more enveloping layers from *Mespilus*. When adventitious shoots are developed from a single layer, these have the pure specific characters proper to the layer without any trace of admixture with the other symbiont.

Nothing is known with certainty of the mode of origin of periclinal chimaeras, but it can hardly be doubted that the growing points of these adventitious shoots are composed of cells derived from the two components, the one forming the core and the other the surface layers.

5. Periodic Changes in Development ($^{104, 105}$).—The development of the organism does not proceed by continuous growth of a uniform activity. Characteristic periodic changes are met with everywhere,

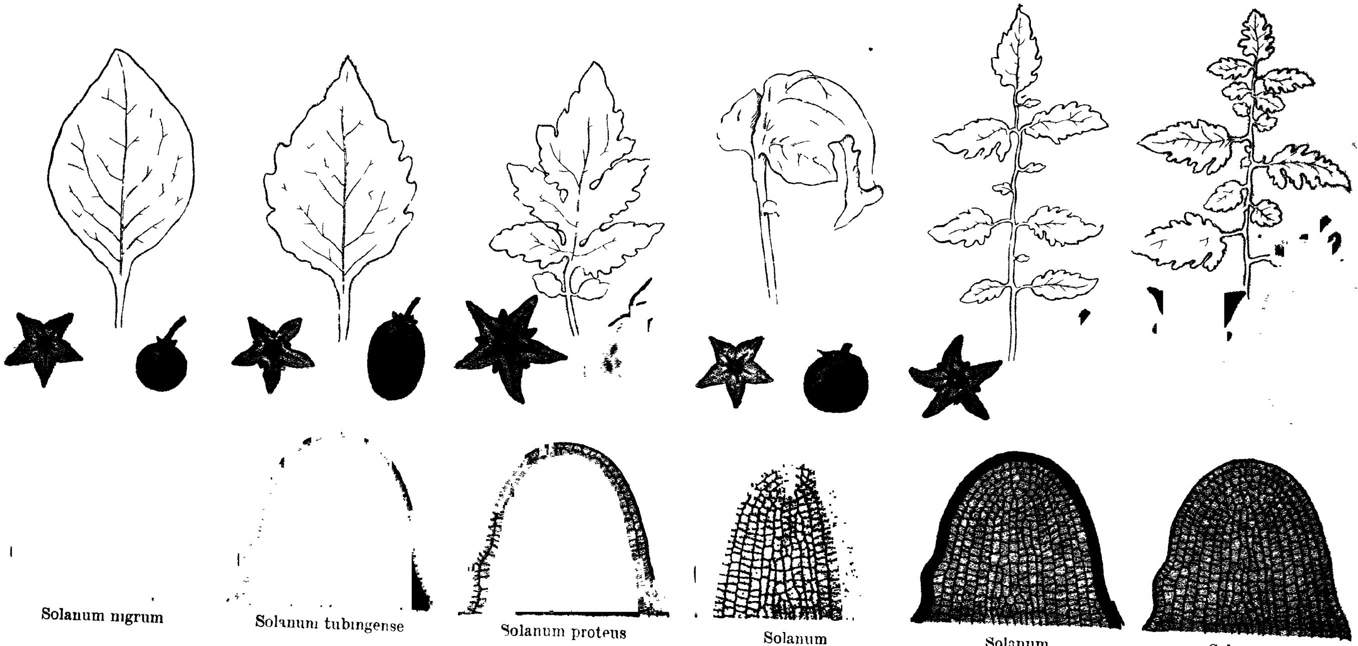


Fig 265 —Chimaeras between *Solanum nigrum* and *Solanum Lycopersicum* together with the parent forms In each case a leaf, a flower, a fruit, and a diagram of the growing poin is represented In the latter the layers derived from *S nigrum* are coloured green, and those from the Tomato yellow. (Original by H Winkler.)

giving rise to phenomena which are closely connected with correlations and are frequently classed with them.

Some examples have already been mentioned. It was noted (p. 279) that the embryonic growth did not go on uniformly but had an underlying rhythm, and the process of elongation can also proceed rhythmically. If, for example, an organ, which has been a long time in the dark and is growing fairly uniformly, is continuously illuminated, what is called the LIGHT-GROWTH REACTION is seen; the previous uniform growth becomes alternately slower and faster, giving a series of waves in the curve.

Fig. 266 shows such a curve for the sporangiophore of *Phycomyces nitens*, a fungus often met with on horse-dung. The sporangiophore has been in the dark to the point marked by the arrow. From this moment it was continuously illuminated by light of a definite intensity and the growth accurately noted at short intervals of time. The previously uniform growth becomes wave-like in the light. The light-growth reaction also appears when the plant is only transiently illuminated with a definite amount of light.

Numerous recent researches have shown that different amounts of light have each their characteristic reaction. This at first glance appears significant in attempting to explain the wavy line of the curve and it would be most important to connect the amounts of light and the undulations of the curve. But the investigations deliberately undertaken, with uniform illumination, show that in the process internal correlative causes must co-operate with the light which acts as a liberating factor. It is necessary to regard the permanent illumination as acting uniformly, just as the preceding darkness did; from this it would have been natural to anticipate a uniform reaction (195).

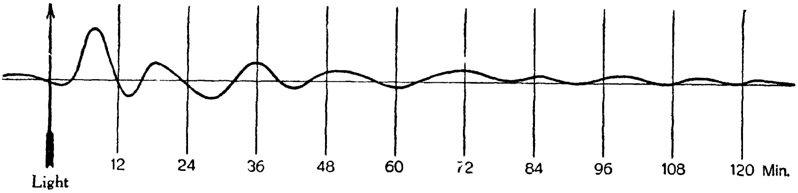


FIG. 266.—Light-growth reaction in the sporangiophore of *Phycomyces*. (After BLAAUW.)

The different organs of the plant behave differently towards illumination. While, for example, in the case of the sporangiophore of *Phycomyces* the growth increases immediately on illumination as is indicated by a rise of the curve to a summit, in the case of the coleoptile of the oat there is first an arresting effect on growth indicated by a trough in the curve. Other factors (temperature, humidity, gravity) behave similarly to light; in relation to them also the plant frequently reacts to a sudden alteration by a periodic reaction.

Some of the most important periodic changes in the development of plants have been mentioned in the morphological part. Thus, in alternation of generations, the sporophyte alternates in a very regular fashion with the gametophyte, which is frequently of quite different morphological construction. There are further periodic changes in the construction of the leaves and stem, which may be qualitative and not merely quantitative; foliage leaves alternate with scale-leaves and bracts, foliage shoots with rhizomes, and the transitions may be gradual or abrupt. In these phenomena also correlations play a part.

The existence, or rather the activity, of a certain quantity of foliage exerts an influence on the primordia forming at the growing point and causes them to develop as bud-scales. If the foliage leaves are removed in early summer these primordia develop as foliage leaves instead of scale-leaves (cf. p. 103). In a similar fashion the removal of leafy shoots may affect a subterranean rhizome, and cause it to grow out of the soil and form foliage leaves instead of scale-leaves.

In addition to the distinction of foliage leaves and scale-leaves heterophylly is met with in some plants (cf. p. 113). It is sometimes possible to bring about a return to the juvenile form when the external conditions under which this arises are again established. Thus in the case of *Campanula rotundifolia* round leaves can be developed on plants which have formed the subsequent linear leaves by diminishing the intensity of the illumination. In some aquatic plants the submerged leaves belong to the juvenile form, and the floating or aerial leaves to the later adult form. Here also the juvenile form can be induced. This is not always the case, however, for sometimes the growing point has been so profoundly changed that it can only produce the later adult type of foliage.

The "shade-leaves" (p. 286) of trees may be associated with juvenile leaves, since their formation depends more on their position on the shoot than on the direct action of the intensity of the illumination. Each shoot commences with shade-leaves and later produces those suited to stronger light. It is evident that nutritive influences play a part in determining these leaf-forms.

The active vegetative period among plants is often succeeded by a period of rest. Thus many trees and shrubs shed their leaves and remain for a time bare. In our climate this happens regularly just before the unfavourable winter season. At first sight it appears as if the resting condition was caused by the climate. As a matter of fact, however, periodic cessations of growth are found in many tropical trees; while temperature and water-supply continue favourable, the leaf-formation does not proceed continuously, but is interrupted by resting periods, so that there are several periods of active growth in the course of the year. In our native plants also the entry upon a resting period is in no way determined by the low temperature. The unfolding of the leaves of many trees ceases completely in May or June. Further, our trees, when transferred to a tropical climate, frequently exhibit a periodicity similar to the native plants of the new locality.

These phenomena are not interpreted in the same way by all investigators. On he one hand it is assumed that every periodicity in the growth of a plant is determined by a periodicity in the environment which need not be in the supply of moisture and warmth, but may concern, for example, the absorption of nutrient salts. On the other hand it may be assumed that plants possess a periodicity depending on internal causes, and that they become adapted to the seasonal changes in countries where such occur; with us the resting period is the winter, while in other countries it occurs in the dry period. This does not hold for all plants, however. In our climate there are some herbs, such as *Senecio vulgaris*, which continue to grow throughout the whole year if the external conditions permit, and in the tropics plants which grow continuously also occur.

The Oak, Beech, Apple, and Pear retain their resting period in the sub-tropical climate of Madeira, while under uniformly favourable conditions in the mountain regions of Java the periodicity may be disturbed in particular individuals. This even occurs in the several branches of the same tree, which may then bear leafy and leafless boughs at the same time (Oaks, Magnolias, Fruit, and Almond trees, together with some endemic species).

IV. Duration of Life (10)

We have further to consider the periodic alternation expressed in the duration of life of the plant as a whole. There are plants, such as *Stellaria media* and *Senecio vulgaris*, which in a few weeks go through their whole development from the germination of the seed to the ripening of their seeds. Since each seed can germinate at once, several generations may be developed within the year. The individual plant dies on producing a certain number of seeds, but the seeds ensure the maintenance of the type of plant. Many annual plants are similar, though their life is more closely connected with the seasons of the year. With these may be placed other plants which only fruit once (monocarpic) but in which seed-formation is preceded by two or many years of purely vegetative growth, with or without resting periods. Probably in all these cases the development of fruit is the cause of the death of the vegetative organs, for their life can be considerably prolonged by preventing seed-formation. In contrast to these plants, others, such as our native trees, fruit repeatedly, the existence of the individual not being terminated by seed-formation. All perennial types exhibit another periodicity besides that due to the seasons. A tree in its first year when it is a seedling has less intensity of growth than many annual plants; the intensity of growth increases gradually and its growth in length, its growth in thickness, and even the size of the elementary organs of the wood continue to increase until a maximum is attained. Some trees attain a great age and are in themselves capable of unlimited life. From a certain point of maximum development, however, the annual shoots become smaller, apparently on account of the increased difficulty of exchange of materials between the roots and leaves. Ultimately the tree dies for this reason, or owing to the attacks of parasites or other disturbing external effects. If care is taken to ensure the production of new roots near the growing points of shoots, the latter will continue to grow with the same intensity, and no termination of the growth is to be anticipated. This experiment cannot be performed on every tree, since some do not readily give rise to roots; it is easily done with the Willow, however, by using branches as cuttings. Long before the whole individual perishes, however, single parts of it have died. Thus the leaves have been shed after persisting for one or several years. In some cases whole branches are shed, though often they perish without being thrown off and gradually break up while still attached to the plant. All the older tissues of the stem also die; the peripheral tissues are transformed into bark and either fall off or form a protective covering to the parts within. In the centre the wood is transformed into heart-wood in which the remaining living elements die. In an old tree only the growing points, whether apical or intercalary, and the youngest tissues derived from them remain alive. Thus we see that every cell which has lost its embryonic character dies after a longer or shorter time. Though this cannot as a rule be prevented, we cannot say that the death is necessary. It is because certain cells develop that others die, and their death is a phenomenon of correlation. In plants that are capable of restitution the removal of the growing point before the permanent tissue has become too old leads to fully-grown cells, which would normally die, becoming embryonic again and continuing to live. Those lower plants with no distinction of embryonic and fully grown cells can continue to grow and divide; death only occurs as the result of unfavourable external factors. In other cases internal factors may have a fatal effect, as in the races of plants which are unable to form chlorophyll and therefore die. In the study of heredity lethal factors can frequently be recognised, *i.e.* determinants which if they became operative would bring about the death of the organism (cf. p. 327, *Oenothera*).

The longevity of trees (107) having an historical interest is naturally best known and most celebrated, although, no doubt, the age of many other trees, still living, dates back far beyond historical times. The celebrated Lime of Neustadt in Wurtemberg is nearly 700 years old. Another Lime 25·7 m. in circumference had 815 annual rings, and the age of a Yew in Braburn (Kent) which is 18 m. in circumference is estimated at 2880 years. *Sequoia gigantea*, the giant tree of California, attains according to H. MAYR the age of 4000 years. A Water Cypress (*Taxodium mexicanum*) near Oaxaca, Mexico, is another well-known example of an old tree (Fig. 624). One of the oldest trees in Germany is an Oak, some 1200 years old, which stands on the Ivenak estate in Mecklenburg, and is about 13 m. in circumference. Bryophytes also may attain a great age; the apically-growing mosses of the calcified *Gymnostomum* clumps, and the stems of the Sphagnaceae, metre-deep in a peat-bog, must certainly continue to live for many centuries.

V. Reproduction

The organs which serve for reproduction have been treated in the section on Morphology. In this place the conditions and the significance of the phenomena have to be considered.

Reproduction commences as a rule when the vegetative growth is slackening and the plant has attained a certain age. In Nature it appears to follow vegetative growth with some degree of necessity. It can, however, be shown that this succession is not obligatory, and that the natural course of development is determined by quite definite conditions, and can be greatly modified by other influences.

1. The Conditions of Reproduction (^{108}).—Thus the question arises, under what conditions does vegetative growth and under what conditions the formation of reproductive organs respectively take place? Since these problems have as yet been relatively little studied, it is not easy to give a general answer to this question. We must, therefore, confine ourselves to making clear the essential facts by means of some examples.

Lower Plants.—The fungi belonging to the genus *Saprolegnia* have a non-septate, branched mycelium without chlorophyll. They occur commonly in Nature on dead insects which have fallen into water, and their thallus first grows through the body of the insect. After a time, however, it grows out and forms a radiating growth around the insect. The end of each of the radiating hyphae becomes as a rule cut off by a septum, and its contents divide up into numerous swarm-spores; these emerge, move about, and finally germinate to give rise in another place to a new individual of *Saprolegnia.* Later sexual organs are formed on the older plant and, at least in some species, the egg-cells only develop after being fertilised. With the production of fertilised eggs the activity of the *Saprolegnia* plant tends to cease; it gradually perishes.

G. KLEBS has shown that it is possible to completely change this course of development of *Saprolegnia*; KLEBS has succeeded in directing the development in the following ways among others:

1. The mycelium can continue for the whole year to grow vegetatively when supplied continually with fresh and suitable nutritive material.

2. Such a well-nourished mycelium on being transferred to pure water proceeds completely and at once to form sporangia.

3. In solutions of leucin (0·1 per cent) and haemoglobin (0·1 per cent) at first a strong growth develops and then sexual organs are formed. Swarm-spores are not formed; they appear, however, after the sexual organs, when a more dilute solution (0·01 per cent) of haemoglobin is employed.

It is thus clear that quite definite conditions exist for vegetative growth, others for the formation of sexual organs, and yet others for the appearance of asexual reproduction.

Conditions of the Formation of Flowers in the Higher Plants (^{109}).—In the Phanerogams asexual reproduction by means of bulbils, etc., is much less prominent than the sexual reproduction which is connected with the flower. While as a rule the production of flowers is associated with the plant having reached a certain age, they may appear on quite young plants. It is thus to be expected that the formation of flowers, as of other organs, will be found to take place under quite definite conditions. The results which **Klebs** obtained with *Sempervivum Funkii* can be summarised thus:

1. With active carbon-assimilation in bright light and rapid absorption of water and nutrient salts, the plant continues to grow purely vegetatively.

2. With active carbon-assimilation in bright light, but with limitation of the absorption of water and salts, the development of flowers takes place.

3. With a moderate absorption of water and nutrient salts it depends on the intensity of the illumination whether vegetative growth or the production of flowers takes place. With weaker intensity of light, and when blue light is used, only growth takes place; with stronger illumination or with red light flowering occurs.

Klebs distinguished three phases in the formation of the flowers of *Sempervivum*.

1. The establishment of the condition of readiness for flower-development. 2. The formation of the primordia of flowers recognisable under the microscope. 3. The enlargement of the inflorescence. These three phases are connected with wholly different conditions and depend therefore in different ways on external factors. The initial condition is determined by a preponderance of carbon-assimilation over processes in which carbohydrates are consumed, such as respiration and vegetative growth. Since a high temperature increases the respiration and nutrient salts promote vegetative growth, a low temperature and a limited supply of nutrient salts are necessary, in addition to good illumination, to render the plant ready to develop flowers. This condition, when once attained, may be destroyed by a high temperature, while it may be preserved for a long while, even in darkness, by a low temperature. While in this respect light apparently acts only in determining the assimilation of CO_2, in the second phase it has another significance; a certain period of illumination is quite indispensable for this, and only the rays of greater wave-length are effective, those of short wave-length even destroying the state reached in the first phase. In Nature the first phase is attained in autumn, but a sufficiently long and intensive illumination is wanting. Under continuous illumination by an Osram lamp, the light from which is rich in red rays, the formation of flowers may be hastened by months; the period is shortened by increasing the intensity of the illumination. The earlier in winter this is done the longer is the illumination required; towards the end of winter as a result of the prolonged low temperature the primordia are so far advanced that a short illumination is sufficient. Interruptions in the illumination must not be too prolonged or the influence of the illuminated period is lost. The third phase of elongation is, like the first, dependent on the nutritive effect of light; in accordance with this, if the preceding nutrition has been sufficient it may, in part at least, be carried out in the dark.

Similar thorough analyses of the conditions of flowering are not available as yet for other cases, but numerous observations and experiments indicate that light, temperature, and the nutrient salts are of primary importance in the formation of the flowers. Since these factors are also indispensable for the vegetative life of the plant, it is the amount in which they are available and especially their relative proportions which determine whether a particular bud shall form a flower or grow vegetatively.

The importance of light in the formation of flowers is shown by the well-known fact that the Ivy only flowers when growing in a well-illuminated situation and not in the shade of woods, although it grows well in the latter habitat. VÖCHTING's experiments on *Mimulus Tilingii* gave the same result. At a certain low intensity of light, which is quite adequate for vegetative growth, this plant produces no flowers. KLEBS has made corresponding experiments with *Veronica Chamaedrys*, and he states that in all plants which do not contain any great amount of reserve materials a diminution of light leads to the suppression of flower-formation. He regards the carbon-assimilation resulting from the illumination as the primary cause of this influence on the development of flowers. At a certain intensity of light, which is insufficient for the development of normal flowers, cleistogamous flowers are produced in some plants.

Temperature also obviously plays an important part. A continuous high temperature hinders flowering. Thus plants of our climate eventually become vegetative in the tropics (Cherry), and native perennial plants, such as the Beet or Foxglove, can be prevented from flowering in their second year if they are kept warm and allowed to grow on during the winter. In this way KLEBS succeeded in keeping the Beet in a purely vegetative state for several years. *Glechoma* and *Sempervivum* also, if their winter rest is prevented, grow vegetatively for years.

Lastly, the nutrient salts have to be considered. By removing the supply of salts, seedlings can often be converted into dwarf starved plants in which, after a few minute foliage leaves have been formed, the development of flowers begins at once. Experiments of MOEBIUS have shown that Grasses and *Borago* flower better if the supply of salts is limited than if well manured. The increase of fertility which results from root-pruning in fruit trees may depend upon a limitation of the absorption of nutrient salts. That, however, all nutrient salts do not act in the same way has been pointed out by BENECKE, who showed both from the literature and from his own experiments that a diminution in nitrogenous food and an increase of phosphorus led to an increase in the development of flowers.

If, after the formation of flowers has commenced, the conditions for vegetative growth are re-established, a shoot already predisposed to flower-formation may again become vegetative. Thus when *Mimulus Tilingii* is brought into conditions of poor illumination the flower-buds already laid down remain undeveloped and resting buds in the axils of bracts develop into leafy shoots. The whole appearance of the plant is thus greatly altered.

2. Fertilisation and its Results.—The product of fusion of the egg and sperm-cell surrounds itself, as a rule, with a cell-wall. In the lower plants an oospore or zygospore is thus formed which germinates, usually after first undergoing a period of rest. In the higher plants growth and cell-division take place forthwith; an embryo is produced which in Bryophyta and Pteridophyta continues its further development, while in the Phanerogams it soon enters on a period of rest. Before this, however, a number of stimuli have proceeded from the development of the embryo; these are especially complex in the Angiosperms. The ovule in which the embryo is enclosed commences to grow; it enlarges and assumes a characteristic structure. It has developed into the seed. The ovary also grows actively after fertilisation and develops into the fruit.

These formative processes of growth in the ovules, ovary, and ultimately also in other parts of the flower, are to be regarded as phenomena of correlation. When fertilisation does not take place, all those changes which lead to the development of a ripe fruit from the flower do not usually occur. Instead another correlative influence arises which leads to the casting-off of the now useless organ as a whole. Some few plants, especially such as have been long cultivated, are to some extent an exception to this. In nearly all varieties of the Banana, in the seedless Orange, and in the Sultana Raisin, no embryo is formed, but in spite of this the fruits develop. The stimulus to this development can proceed either from the mere pollination of the stigma or from the fertilisation of the ovules, which then sooner or later cease to develop without arresting the development of the fruit. In some cases, however, "barren" fruits develop wholly without the stimulus of pollination (parthenocarpic (110) fruits of the Fig, Cucumber, and certain species of Apple and Pear). Influences which affect parts at a distance also proceed from the pollen-grains and pollen-tubes on the stigma. Thus after the stigma of an Orchid is pollinated the stigma and the gynostemium swell, and the perianth is promptly arrested in its growth and withers. As FITTING (111) showed, this influence proceeds from soluble organic substances which withstand heating, and can be readily separated from the mass of ungerminated pollen.

Whether a simple spore or a complex embryo is the result of fertilisation it is always distinguished from the cells which gave rise to it by having nuclei which contain the diploid number of chromosomes (p. 189) On this account a reduction-division which restores the normal number of chromosomes is sooner or later the necessary sequel to fertilisation.

3. The Significance of Sexual Reproduction.—The significance of sexual reproduction is not at once evident. Many plants occur in Nature or under cultivation without being sexually reproduced, and succeed with vegetative reproduction only.

Lower plants which have not attained to sexual reproduction have already been referred to (p. 184). Of higher plants which no longer produce descendants sexually the cultivated Bananas, *Calamus*, some Dioscoreaceae, some forms of Vine, Oranges, and Strawberry, and *Mentha piperita* may be mentioned. The Garlic, which forms small bulbils in place of flowers, the White Lily, and *Ranunculus Ficaria*, which has root-tubers, only rarely produce fertile seeds if allowed to form their vegetative organs of reproduction. Under certain conditions, as for instance on cut inflorescences, seeds may be produced, though as a rule these plants are multiplied entirely vegetatively. No degeneration such as was formerly held to be unavoidably associated with purely vegetative multiplication is to be observed in these cases (112).

If thus the monogenic reproduction suffices to maintain the species, digenic reproduction must serve some further purpose not effected by the former. Otherwise it would be inconceivable why digenic reproduction had arisen, and why the arrangements to effect it are far more complicated and less certain than in the case of vegetative reproduction.

Were the Algae and Fungi alone taken into consideration it might be supposed that sexual reproduction led to the formation of specially resistant germs which could endure a longer period of rest under unfavourable conditions—as a matter of fact, the zygospores and oospores are frequently much more resistant than the swarm-spores and conidia. But even in the Pteridophyta this relation is inverted, for the fertilised egg-cell requires to develop forthwith, or else it perishes, while the asexual spores can endure a long resting period.

It is the rule in digenic reproduction that the sexual cells are individually incapable of development; this takes place only after the sexual cells have united. Thus one use of fertilisation lies in the removal of an arrest of growth, though it cannot be said that this was its original and essential significance. It is much more probable that the sexual cells have gradually lost the capacity of independent development since in this way the possibility of fusion was increased. If every sexual cell commenced to grow at once, this would in most cases take place before fusion with another sexual cell could be effected.

This assumption is supported by the behaviour of some Algae, in which the sexual cells can often germinate independently; the egg-cells especially may develop without fertilisation (PARTHENOGENESIS). In the primitive Algae parthenogenesis is possible, because in them the incapacity of development of the egg-cell has either not been acquired or is easily removed under special conditions. Thus, for example, in the Alga *Protosiphon* parthenogenetic development is induced by a high temperature, and the same happens in the case of the ova of some lower animals (Echinoderms) on treatment with solutions of a certain concentration. It may perhaps be assumed that in the cases in which development only takes place after fertilisation the stimulus to development is given by some substance contained in the sperm-cell.

We thus arrive at the conclusion that the essential of sexual reproduction cannot consist in the removal of the arrest to development of the sexual cells. This leads us to consider THE FUSION OF THE SUBSTANCE OF THE TWO CELLS AND THE MINGLING OF PATERNAL AND MATERNAL CHARACTERS WHICH FOLLOWS FROM THIS. This brings out the chief distinction between the two modes of reproduction; the vegetatively produced progeny are due to no such mingling of characters. The complex of characters in vegetative multiplication does not differ as a rule from that in the parent form. As a matter of fact, we preserve by vegetative multiplication all the varieties and races of our cultivated plants, even when these do not come true from sexually produced seed. In contrast to the vegetative progeny the sexually produced descendants, as a rule, cannot completely resemble the mother-plant, but must combine the characters of both parents. The more these differ from each other, the more striking will be the visible effect of fertilisation.

VI. Heredity, Variability, Origin of Species

Heredity (^{114}).—By inheritance is understood the familiar phenomenon that the properties of the parents are repeated in their progeny. This phenomenon is presented to us in the division of a cell, which is the simplest form of reproduction, as well as in the more complicated process of sexual reproduction. That the daughter-cells resemble the parent-cells requires no explanation. The problem of heredity appears when descendants are derived from the GERMS, which are small portions of a complicated parent organism, by a process of DEVELOPMENT. It is assumed that such germs possess DETERMINANTS or GENES, which determine that an organism shall develop in a definite specific way. It appears probable that these determinants are associated in the chromosomes of the nucleus, but we know nothing as to the way in which they influence the course of development.

Such determinants must be present in the sexual cells of the higher plants, and both in the male and the female cells. The fertilised egg-cell must thus possess a double number of these, though a single organism is derived from it. That, originally at least, the same determinants are present in all cells of the plant and not only in the germ-cells is shown by the phenomena of restitution

The problems of inheritance are of greatest interest in sexual reproduction, in which the part played by the two parents in the organisation of the progeny comes into prominence. These problems can only be attacked by a consideration of hybrids, where there is a difference in the determinants of the two parents.

Hybrids (115).—The union of two sexual cells is, as a rule, only possible when they are derived from individuals of the same species; it is only then that they fuse together in the act of sexual reproduction. Occasionally, however, the sexual cells of different varieties, species, or even genera have been shown to be able to unite and produce descendants capable of development. Such a union is termed HYBRIDISATION, and its products HYBRIDS. They are also spoken of as HETEROZYGOTES or individuals derived from two dissimilar sexual cells, in contrast to HOMOZYGOTES, which have arisen from the union of sexual cells with identical determinants. Hybrids are as a rule obtained more readily the closer the parent forms are to one another, but this is not a rule without exceptions.

The phenomenon known as XENIA can be understood in the light of the fact that not only the egg but also the nucleus of the embryo-sac fuses with a male nucleus. In this way hybrid heterozygotic endosperms result from the fusion of the nuclei if these possess unlike determinants.

Some families exhibit a tendency to hybridisation (Solanaceae, Caryophyllaceae, Iridaceae, etc.) while in others hybrids are obtained with difficulty or not at all (Papilionaceae, Coniferae, Umbelliferae, etc.). The behaviour of related genera and species also is frequently very different. Thus species of *Dianthus*, *Nicotiana*, *Verbascum*, and *Geum* readily hybridise with one another, while those of *Silene*, *Solanum*, *Linaria*, and *Potentilla* are difficult to hybridise. Hybridisation of closely related species may frequently fail when more distant species can be crossed.

Hybrids also occur in Nature, especially in the genera *Salix*, *Rubus*, *Hieracium*, and *Cirsium*. That such natural hybrids do not occur oftener is due to the lack of an opportune time or space for their development, and also to the fact that in the case of pollination of flowers with different kinds of pollen, that of their own species seems as a rule more effectual in effecting fertilisation.

Hybrids are often recognisable by having the characters of intermediate forms between the two parents. They may either be truly intermediate, *e.g.* *Nicotiana rustica* ♀ × *Nic. paniculata* ♂ and *Sorbus aria* × *S. aucuparia* (Fig. 267), or may in some characters resemble more closely the male parent and in others the female parent. In exceptional cases a hybrid may, even to minute characters, resemble the male parent (some hybrids of the Strawberry) or the female parent. In the great majority of cases it is immaterial which plant is taken as the male and which as the female parent (reciprocal hybrids). In some cases, however, the hybrid A ♀ × B ♂ is clearly different from A ♂ × B ♀.

The mingling of characters is often complete. When one species has simple and the other compound leaves, their hybrid may have leaves more or less cleft (Fig. 267); or if the flowers of one parent species are red and those of the other yellow, the hybrid frequently bears flowers which are orange-coloured. If an early blooming form is crossed with a late bloomer, the hybrid may flower at a time intermediate between the two.

New characters frequently appear in hybrids such as diminished fertility, a greater tendency to the formation of varieties, and frequently a more luxuriant growth.

The fertility is often so enfeebled that the hybrids either do not flower (*Rhododendron*, *Epilobium*), or are sterile and do not reproduce themselves sexually. This enfeeblement of the sexuality generally increases the more remote is the relationship of the ancestral forms. Other hybrids such as those of *Salix* and *Hieracium* remain fertile.

Hybrids, particularly those from nearly related parents, frequently produce more vigorous vegetative organs, they bloom earlier, longer, and more profusely than the uncrossed plants, while at the same time the flowers are larger, more brilliant, and exhibit a tendency to become double. The luxuriance of growth and the increased tendency to produce varieties displayed by the hybrids have made the whole subject of hybridisation one of great practical importance for horticulture and agriculture.

Inheritance in Hybrids (116).—By the experimental study of hybridisation, the sexuality of plants, for a long time doubted, was indisputably proven. With this object in view, hybrids were raised in great numbers by KÖLREUTER as early as 1761. It is now the problems of inheritance connected with hybridisation that are the main centres of interest. For the study of heredity, however, hybrids between species are far too complicated. It was by using closely related forms that GREGOR MENDEL at Brünn discovered in 1866 certain laws, which, however, did not attract attention or influence the progress of investigation till after 1900. At this

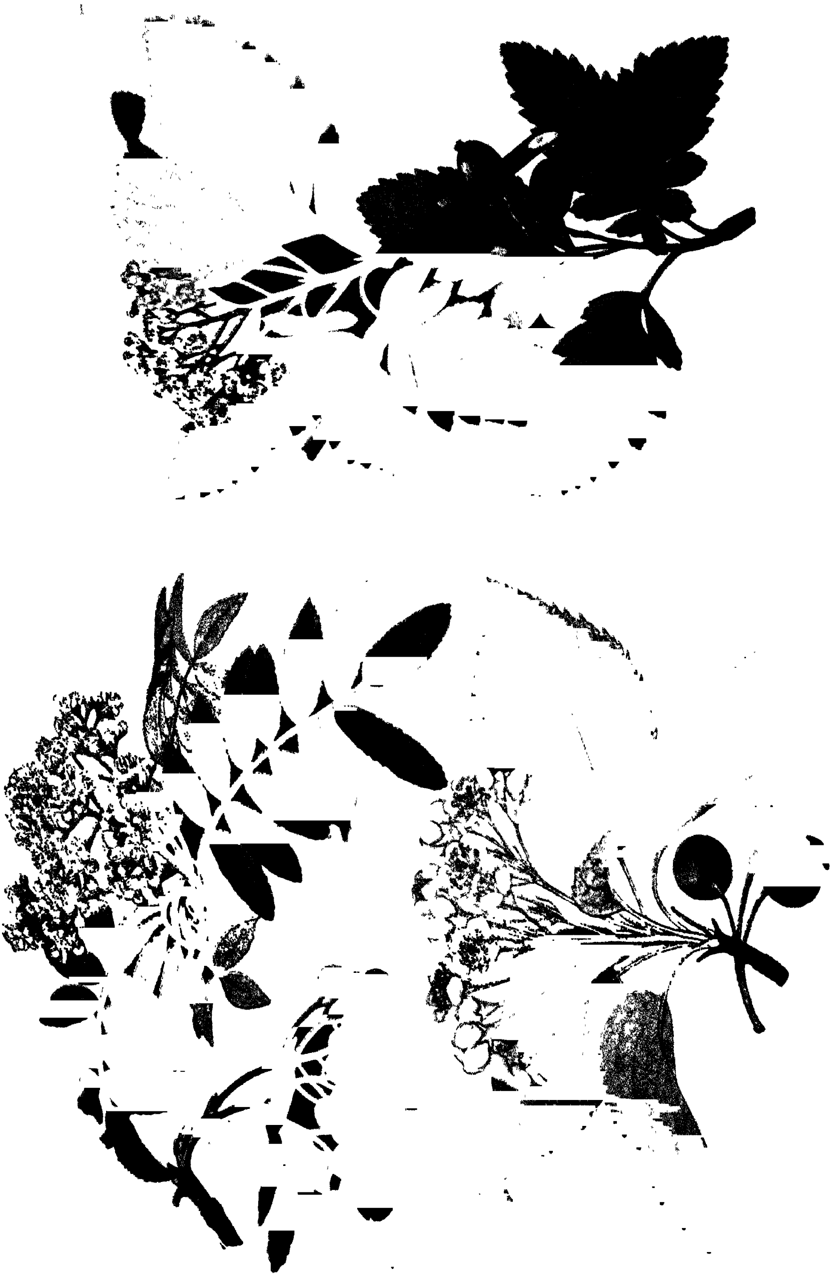


FIG. 267.—1. *Sorbus aucuparia.* 2. *Sorbus aria.* 3. The hybrid between these. (After SCHLECHTENDAL, LANGETHAL and SCHENK: *Flora von Deutschland*, 5th ed. by HALLIER.)

date they were re-discovered simultaneously by De Vries, Correns, and Tschermak. In order to obtain these laws or rules Mendel required to follow the behaviour of the hybrids through a number of generations, taking statistical account of all the individuals that result.

1. Law of the Uniformity of Hybrids.—When both the parents are homozygotic all the hybrids in the first (F_1) generation are alike. They may either be intermediate in character between the parents (intermediate inheritance), or they may almost or quite completely resemble one of the parents (dominant or prevalent inheritance).

An example of intermediate inheritance is afforded by the hybrids between *Mirabilis jalapa rosea*, and *M. jalapa alba*, two races of this plant belonging to the Nyctaginaceae, which only differ in the white or red colour of the flowers (Fig. 268). The hybrid between two stinging nettles, *Urtica pilulifera* and *U. dodartii*, is an example of dominant inheritance; the former has markedly serrate leaves, while these are almost entire in *U. dodartii*. In this case the first hybrid generation can hardly be distinguished from *U. pilulifera*, since all the plants have the serrate type of leaf (Fig. 269). It required a detailed investigation by Correns to show that there was a slight difference, at least in the young plants, between the hybrid and this parent form. In this case *Urtica pilulifera* is said to behave as the dominant form, while *U. dodartii* is the recessive. It is impossible to

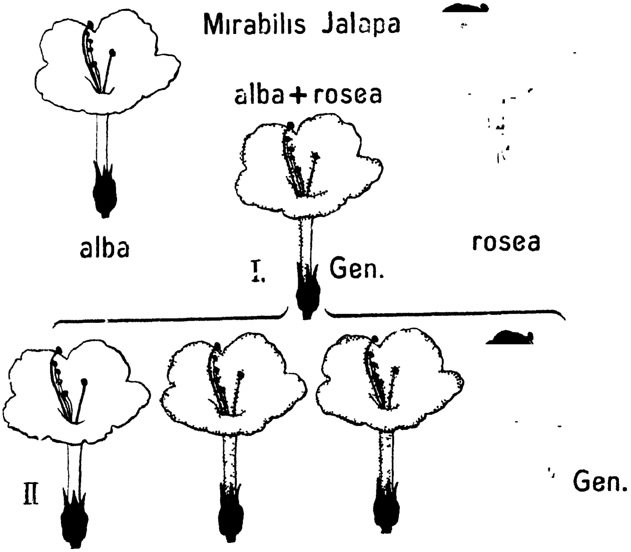


Fig. 268.—*Mirabilis jalapa*, *alba* and *rosea*. With the hybrid between them in the first and second generation. (Diagram after Correns.)

predict which characters will dominate in inheritance, and only experience can decide the point.

2. LAW OF SEGREGATION.—In the second (F_2) generation obtained by the pollination of flowers of the F_1 with pollen from among themselves the plants are no longer all alike, but are of different types that appear in regular proportions. In the simplest cases, such as those of *Mirabilis* and *Urtica* described above, where the parents differ in a single character, the regular composition of the F_2 generation is readily recognised. In *Mirabilis* three types appear in definite proportions, 50 per cent which have the characters of the plants of the first hybrid generation, 25 per cent resembling the one parent-plant and 25 per cent the other. When the plants flower these three groups have rose coloured, red, and white flowers respectively (Fig. 268). To the extent of one-half of the progeny the characters of the hybrid have segregated, so that one quarter of the progeny are pure paternal plants and one quarter are pure and resemble the original female parent; only the remaining half are of hybrid nature. The correctness of this interpretation is shown in the third and following generations; it is found that the red- or white flowered plants of the second generation when self-pollinated reproduce their type truly, while the progeny of the plants with rose-coloured flowers segregate

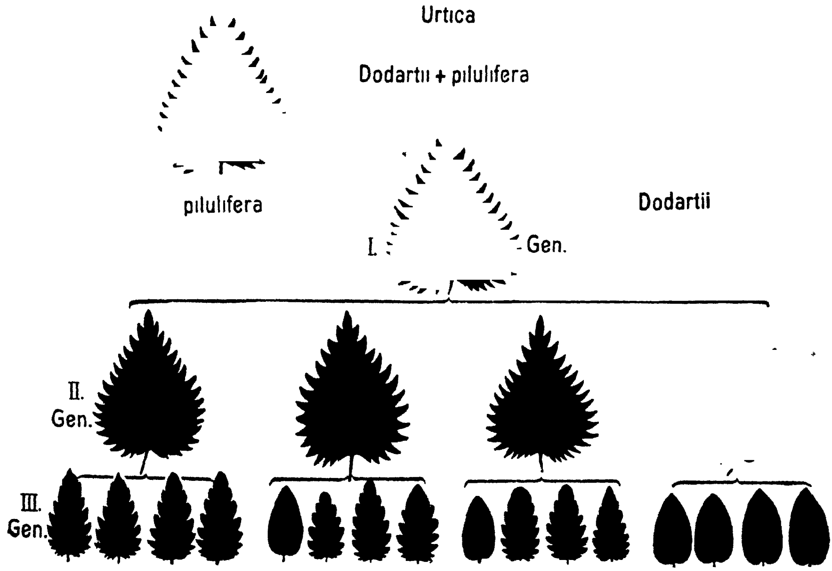


FIG. 269.—The hybrid between *Urtica pilulifera* and *Urtica Dodartii* in three generations. (Diagram. After CORRENS.)

in the same proportions as before. The phenomenon is termed the segregation of hybrids. In successive generations the hybrids with rose-coloured flowers form a diminishing proportion of the total progeny while that of the red- and white-flowered plants increases. In the eighth generation there will be only 0·75 per cent hybrids, and this small proportion continues to diminish with segregation.

When one of the characters is dominant the appearances resulting from segregation are somewhat different, as is shown for *Urtica* in Fig. 270. In the second generation 25 per cent of the plants resemble *U. dodartii*, and are found to breed true in subsequent generations; 75 per cent have the characters of *U. pilulifera*, but the test of further breeding shows that these are not all of the same type; one third of them are pure *U. pilulifera*, while two-thirds prove to be of hybrid nature. The latter in the next generation segregate in the same apparent proportions as in the second generation, *i.e.* 3 : 1.

The explanation of the law of segregation since the time of MENDEL has been on the lines of assuming that the unlike determinants present in the heterozygotic hybrid separate in the formation of the sexual cells. Thus the sexual cells of the rose-flowered hybrid *Mirabilis* no longer possess the hybrid character, but are divided into one-half "red" and one-half "white" homozygotic gametes. In the fusions at fertilisation the combinations leading to the production of hybrids, red × white (white ♀ × red ♂, red ♀ × white ♂) will be twice as numerous as the combinations red × red or white × white.

The facts in such questions of inheritance can be conveniently represented by means of symbols. The individual determinants or genes are denoted by letters. If a particular plant has the determinants A, B, C, D ... X, its descendants in a pure culture will have the genetic formula AA, BB, CC, DD ... XX, since the same determinants are contributed by both the father and the mother. If, however, the two germ-cells differ as regards one determinant, the descendant will be heterozygotic in respect of this. Thus if the determinant for the red colour in *Mirabilis* is denoted by R, the corresponding not-red (*i.e.* white) gene will be denoted by r.

In this particular case it would be equally natural to employ the capital letter for the determinant for white, and to denote red, or not-white, by the small letter. When, however, one of the characters is dominant it is always denoted by the capital letter and the corresponding recessive character by the small letter.

If, therefore, all pairs of like characters are omitted the symbolic representation for the inheritance in the case of *Mirabilis* takes the following form :

Parents	RR (red)	rr (white)
the sexual cells of which	♂ 100% R ♀ 100% R	♂ 100% r ♀ 100% r
Hybrid 1st Generation	Rr (rose)	
the sexual cells of which	♂ 50% R ♀ 50% R	♂ 50% r ♀ 50% r
Combinations of these	RR, Rr, rR, rr.	

The last line shows the segregation which will be evident in the second generation: 25 per cent RR will have red flowers, 25 per cent rr will have white flowers; both are homozygotes. Fifty per cent, however, are heterozygotes, Rr, and these will have rose-coloured flowers and will in turn segregate. If, however, red were dominant to white it could be inferred from this line that in the second generation 25 per cent white-flowered and 75 per cent red-flowered plants would arise, and that one-third of the latter would be homozygotic and two-thirds heterozygotic.

3. LAW OF THE AUTONOMY OF CHARACTERS.—When the parents differ in two characters instead of only one, dihybrids instead of monohybrids result. It then appears that the two characters which are connected with one another in the homozygotic parents separate from one another in the process of segregation and are distributed independently in the progeny (AUTONOMY OF CHARACTERS). Thus new COMBINATIONS OF CHARACTERS come about in the F_2 generation, a fact of great importance both in plant-breeding and in the behaviour of plants in Nature. From crossing a variety of maize with smooth white grains and one with wrinkled blue grains, races with smooth blue and wrinkled white grains arise as new combinations.

This result can readily be arrived at by considering the following symbolic representation. Since smooth is dominant to wrinkled they are denoted by S and s respectively: similarly since blue is dominant to white they are written as B and b respectively.

Parents	Sb			sB
1st Generation		Ss Bb smooth blue		
Germ cells of this	SB	Sb	sB	sb

Combinations of these germ cells:

SB **SB** **smooth** **blue**	SB SB smooth blue	SB sB smooth blue	SB sb smooth blue
Sb SB smooth blue	**Sb** **Sb** **smooth** **white**	Sb sB smooth blue	Sb sb smooth white
sB SB smooth blue	sB Sb smooth blue	**sB** **sB** **wrinkled** **blue**	sB sb wrinkled blue
sb SB smooth blue	sb Sb smooth white	sb sB wrinkled blue	**sb** **sb** **wrinkled** **white**

It can be ascertained from this scheme that the following segregation has taken place:

9 smooth blue; 3 smooth white; 3 wrinkled blue; 1 wrinkled white.

The symbols further show that only 4 of the 16 combinations are homozygotic, viz.:

SB Sb sB sb
SB Sb sB sb.

The 12 other combinations are heterozygotic and will segregate in the next generation.

The most important conclusion to be drawn from these investigations into heredity is this: THAT TWO ORGANISMS WITH QUITE DIFFERENT DETERMINANTS MAY APPEAR QUITE SIMILAR; THE TYPE EVIDENT TO EXTERNAL OBSERVATION (PHENOTYPE) MAY BE ALIKE IN THE TWO AND YET THE TYPE AS REGARDS THE DETERMINANTS (GENOTYPE) BE DIFFERENT. THUS ONLY BY GENETIC ANALYSIS AND NOT FROM EXTERNAL APPEARANCE CAN THE EQUIPMENT OF DETERMINANTS BE DISCOVERED.

Back-Crossing.—The result of crossing a hybrid with one of the parent forms can be most easily understood by employing the symbolic notation. If a plant AA is crossed with the hybrid Aa the former will produce germ-cells of the one kind A, while the germ-cells of the hybrid will be A and a. It follows that in 50 per cent of the cases A will meet with A and in the other 50 per cent A with a. Half of the resulting plants will therefore be of hybrid nature and half of the type of the pure parent form.

Determination of Sex (117).—It has been found that the inheritance of sex in dioecious plants follows the scheme for crossing back just considered. The fundamental investigations on this point are those of CORRENS, who crossed the dioecious *Bryonia dioica* with the monoecious *Bryonia alba.* The female flowers of *Bryonia alba*, when fertilised by the pollen of *Bryonia dioica*, gave 50 per cent male plants and 50 per cent female plants. CORRENS' explanation of this result is based on regarding dioecious plants as consisting in a sense of two strains which can only be maintained by crossing. The male character is dominant, the female recessive, in a cross. Female plants must be homozygotic for the sex factors (aa) and produce only one type of sexual cell (a); the male plants are heterozygotic (Aa) and their sexual cells as a result of segregation are of two kinds, viz., 50 per cent A and 50 per cent a. As in the back-crossing of a hybrid with one of its parent forms, the result of fertilisation will here be that in half the cases the factors aa are combined, which gives female-plants; and in half the cases the factors A and a, which, since A is dominant, gives male plants. The assumption that the female plant is homozygotic with the genetic formula aa, and the male plant heterozygotic with the formula Aa, explains why the two sexes are met with in Nature in approximately equal numbers. Since there is no means of influencing the pairing of the sexual cells, this proportion cannot be modified experimentally. CORRENS has, however, been fortunate enough to do this in some other cases, *e.g. Melandrium.* If the stigma of this plant is pollinated with relatively little pollen, 43 per cent of male plants are obtained, but only 30 per cent if a large amount of pollen is used. CORRENS explains this by the pollen-tubes of the pollen-grains with the determinant a, those that give rise to female-plants, growing more quickly. When there is an excess of pollen there is a competition between the two kinds of pollen-tubes; those that grow more rapidly being more likely to effect fertilisation than the slower growing tubes. The two types of pollen-grain can also be distinguished in other ways, *e.g.* by their resistance to heat and to alcohol.

Numerous investigations in recent years indicate that sex is determined in different ways in the various groups of plants. In the Archegoniatae and Spermatophyta four types may be distinguished, as CORRENS has pointed out.

Type. 1. The simplest relations are found in monoecious Bryophyta and the Ferns. Every cell is capable of giving rise to male and female sexual organs (antheridia and archegonia).

Type 2. In hermaphrodite or monoecious flowering-plants, the relations which exist can be represented in the same way.

Type 3. In dioecious Bryophyta the case is different, for here the separation of male and female plants has already taken place in the spores. At the reduction division each spore-mother-cell gives rise to two ♂ and two ♀ spores.

Type 4. The same holds for dioecious Flowering Plants, which have been considered above.

Validity of the Three Mendelian Laws.—These rules are not limited to hybrids in the narrow sense of the word, but have an extensive application to inheritance in both the animal and vegetable kingdoms. It cannot be said that there are not other laws followed in inheritance, for there are already well-investigated cases which do not conform to the Mendelian laws (118). On the other hand, it is noteworthy that many phenomena which at first appeared to contradict these rules have proved on further investigation to be consistent with them.

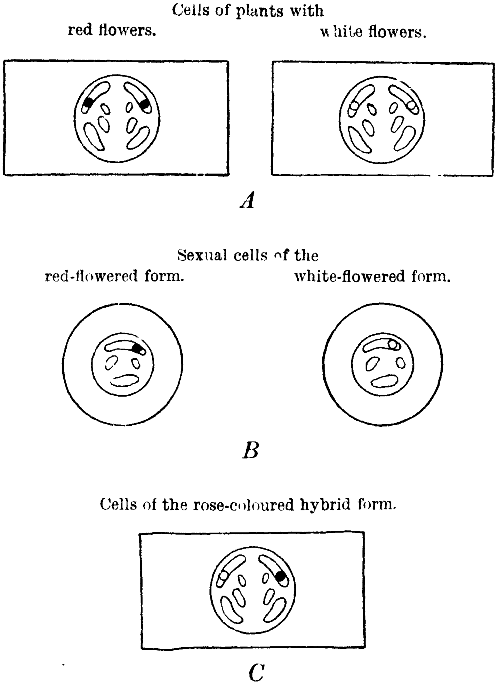
Some facts which at first sight are difficult to understand can be explained on Mendelian lines. Thus it has been observed that the hybrid between a white-flowered and a pale yellow *Antirrhinum* does not have very pale yellow flowers, but these are red. In the second generation segregation, as usual, occurs; there result 3 red, 6 pale red, 3 pale yellow, and 4 white-flowered plants. The full explanation of this cannot be given here, but the case is cited to indicate that the red colour is without doubt that of the ancestral form from which both the white and the pale yellow varieties have been derived. Thus in hybridisation ancestral characters may reappear (atavism); this is a frequent experience of breeders.

The Chromosomes as Bearers of the Segregating Genes (119).—The chromosomes are shown by numerous investigations to be of importance as bearing the material on which inheritance depends, *i.e.* as containing the genes (cf. p. 188). From this consideration the Mendelian laws, especially that of segregation, can be very simply understood, as may be shown by the following example (Fig. 270).

Mirabilis has 16 chromosomes in its somatic cells, but for simplicity only 8 are represented in the figures. The hereditary factors for red and white are regarded as localised in the largest of the chromosomes, the determinant for red being represented by a black dot and that for white by a circle of corresponding size. The diploid hybrid plant produced on fertilisation has derived four chromosomes from the father and four from the mother; among its determinants are therefore one with the determinant for red and one with the determinant for white flowers, and this is expressed by the rose-coloured flowers. The phenomenon of segregation, when the hybrid is self-pollinated, can readily be understood in the same way.

There are many genes in a chromosome. In every plant therefore there are groups of genes which by reason of their position in a chromosome are linked together. Typical segregation can only be shown by such genes as are situated in different chromosomes. Recent researches, especially of Morgan and his school, have demonstrated that there are really only as many groups of genes which can segregate independently as there are chromosomes.

In the reduction division there is a separation of entire chromosomes. It may happen that the original chromosomes before the separation is effected do not lie parallel and that the longitudinal division then results in the new chromosomes being each composed of halves from the two original chromosomes, as is illustrated by the diagram in Fig. 271. This phenomenon, which is of great importance in genetics is known as "crossing over" (120).


Cells of plants with
red flowers. white flowers.

Sexual cells of the
red-flowered form. white-flowered form.

Cells of the rose-coloured hybrid form.

FIG. 270.—The chromosomes in the crossing of red and white forms of *Mirabilis jalapa*. (After GOLDSCHMIDT.)

Variability (121).—By variability is understood the fact that the individuals belonging to any species are not all alike. Frequently the variability is only apparent, the species not having been properly defined. Thus in *Rosa*, *Rubus*, *Draba verna*, etc., there are many species that closely resemble one another. The impression given of a "varying" species is in these cases a completely false one; each of the "ELEMENTARY SPECIES", of which the "COLLECTIVE SPECIES" is composed, proves to be constant and does not exhibit transitions to the other elementary species. Such cases are to be left out of consideration here. We are concerned with the most strictly limited species, if possible with the descendants of a single self-fertilised and therefore homozygotic plant constituting what is known as a pure line (JOHANNSEN). It is found that these also vary. The process of variation and the varieties can be traced to two causes and are therefore distinguished as MODIFICATIONS and MUTATIONS. To these must be added the COMBINATIONS originating from crossing.

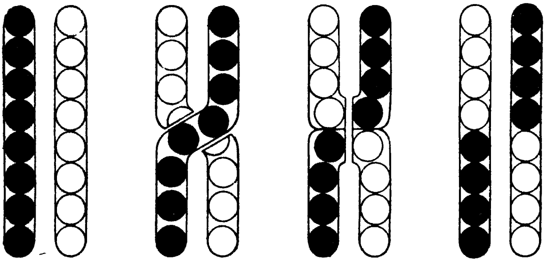


FIG 271.—Diagrams to illustrate "crossing over".

MODIFICATIONS.—This name is given to variations which have been produced by external factors. It has already been pointed out (p. 283 ff.) in what way innumerable external factors influence the form of the plant In order to ascertain the full capacity for modification of any plant it is necessary to cultivate it under all conditions under which it can exist. Such investigations have been carried out with success by KLEBS. If it were possible to grow two plants of the same origin under completely identical conditions they would necessarily be indistinguishable. In practice this is never possible, and therefore the homozygotic individuals of a pure line show many quantitative differences even under the most uniform cultivation possible. For example, the seeds of a pure line of Bean can be sorted into a number of groups according to their weights, and the number in each group or category ascertained. The result of such an investigation is the curve in Fig. 272, which shows that the weight-categories that occur most frequently are those closest to the average weight, and that the farther a category is from the average the fewer are the individuals belonging to it. Practically all statistical investigations of variation conform to this result. The VARIATION CURVES thus obtained agree more or less closely with the so-called curve of chance. This is readily understood, for there are always several external factors acting which may result in either an increase or diminution of the size, number, or weight of the beans under consideration. Only chance decides which effect takes place. Thus only rarely will all the factors make for diminution or all the factors for increase; more frequently the factors will be combined so as to determine an intermediate result. If a seed of a pure line is sown it is indifferent whether one starts from a small, medium, or large specimen. The variation curve of the next generation will not differ from that of the generation to which the seed belonged. Such modifications persist only as long as, or but little longer than, the action of the causes giving rise to them.

Practical experience seems at first sight to contradict this result. In the process of SELECTION a plant with special properties is chosen from a large number and the same characters appear to recur frequently in its descendants. This depends on the fact that in this case a single pure line has been isolated from what was really a mixture of a number of different races or lines. The characteristic properties of the selected line are continued in the descendants. If the material to begin with is really pure, selection has no effect.

COMBINATIONS.—Pure lines can only be maintained by continuing self-fertilisation or by vegetative propagation. On cross-pollination, even between the pure lines of the same species, heterozygotes usually result. The determinants and characters of the pure lines are variously mingled in such individuals. This form of variation is superficially not distinguishable from modification, for it may also show the curve of chance. It is, however, essentially different; for the different individuals have arisen by the mingling of determinants and their subsequent segregation according to Mendelian laws. This form of variation, which is inheritable, is termed combination.

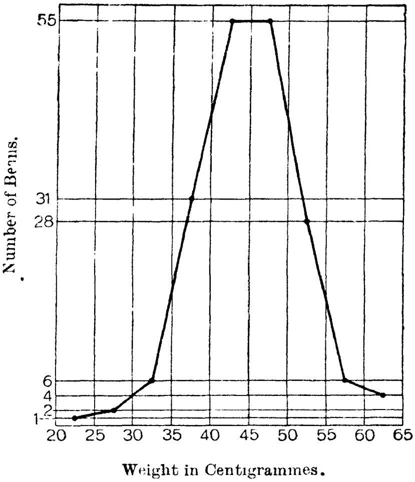


FIG. 272.—Variation curve of the weights of Beans of a pure line (JOHANNSEN'S Line K). (After BAUR.)

MUTATIONS (122) are variations that are distinguished from combinations in not having arisen by hybridisation, but resemble them in being inherited. Mutations can only be recognised with certainty under experimental conditions when in the descendants of a pure line individuals appear which possess a new character or are wanting in a character of the parent organism, the departure being maintained in their offspring. The appearance of such mutations has been frequently observed in cultures. BAUR found on an average 2 per cent of mutants in the seedlings of his cultures of *Antirrhinum.* It is also highly probable that many variations met with in Nature should be regarded as mutations. Thus, for example, *Chelidonium laciniatum,* a mutation of *Chelidonium majus* with incised leaves, was found at Heidelberg in 1590 (Fig. 273). *Fragraria monophylla,* which was first noticed in 1761, differs from the ancestral form of the Strawberry in having simple instead of trifoliate leaves. The remarkable *Nicotiana tabacum virginica apetala,* which arose in a culture of KLEBS, must be placed here. Many such mutations have appeared more than once, and this holds also for mutants arising in cultures. Mutants remain constant if self-pollinated. These forms usually only differ from the parent form in a single character. In the great majority of cases this behaves as a recessive character when the mutant is crossed with the form from which it arose. But mutations are also known which behave as dominants.

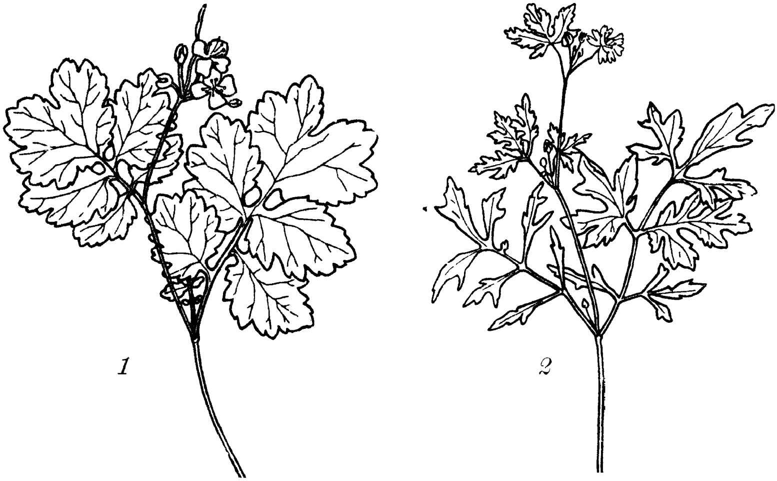


FIG. 273.—Habit of *1, Chelidonium majus*; *2, Chelidonium majus laciniatum.* (After LEHMANN.)

Many cultivated plants are mutations in a single character The incised-leaved form already mentioned is of this nature. Other examples are the races of trees with weeping or pyramidal growth, and plants with narrow, curly, or reddish leaves. These make their appearance especially as seedlings, but in some cases arise vegetatively as lateral branches (vegetative mutation).

It is easy to see that such forms will usually be heterozygotic. If of sexual origin they can only be homozygotic when both the sexual cells concerned had mutated in the same way ; if of vegetative origin only if the mutation affects alike the two corresponding genes of a diploid cell. Both these occurrences will obviously be exceptional. Thus in the cultures of *Antirrhinum*, already referred to, BAUR found only 0·05 homozygotic mutants per 1000 seedlings.

Other mutations are known, some of which differ profoundly from those dealt with above. It is only possible to mention here the fact that a mutant may differ from the parent form in the number of its chromosomes. Thus these may be doubled and the difference may be manifested in the increased size of the plant. A special category of mutation-like variations are those known in *Oenothera lamarckiana* (^{122a}) and some other species of the genus. They are of historical interest for it was in them that DE VRIES first observed the origin of new forms. But it is difficult now to term these variants true mutations, since *Oenothera lamarckiana* is evidently a hybrid with the peculiarity that its parent forms are no longer capable of existence.

Origin of Species (^{123}).—It is only to be noted in this place that, so far as can be seen at present, only mutations and combinations can be concerned in the production of species, since they only are inherited.

SECTION III

MOVEMENT

Phenomena of movement are met with in the living plant not less generally than those of metabolism and development. Metabolism is associated with a continual movement of the raw food-materials, which are absorbed, and of the products of metabolism. These movements have already been dealt with sufficiently in the first section. In addition there exist a number of visible alterations of position exhibited either by the whole plant or by its several organs; these movements are, it is true, often very slow but sometimes are quite sudden.

PROTOPLASM itself is capable of different movements both in the naked condition and when enclosed by a cell-wall (cf. p. 12). Multicellular plants, however, as a rule ultimately attach themselves, by means of roots or other organs, to the place of germination, and so lose for ever their power of change of position. Instead of this they usually possess the power of changing the position and direction of their organs by means of CURVATURE. In this way the organs are brought into positions necessary or advantageous for the performance of their functions. By this means, for example, the stems are directed upwards, the roots downwards; the upper sides of the leaves are turned towards the light, climbing plants and tendrils twined about a support, and the stems of seedlings so curved that they break through the soil without injury to the young leaves.

Movements of locomotion and movements of curvature have thus to be distinguished.

I. MOVEMENTS OF LOCOMOTION (124)

A. Mechanism of Movements of Locomotion

Changes of position are brought about by AMOEBOID MOVEMENT, CILIARY MOVEMENT, and the MOVEMENT OF PROTOPLASM IN CELLS WITH CELL-WALLS.

The creeping movements of naked protoplasts, such as are shown by an amoeba or plasmodium, in the protrusion, from one or more sides, of protuberances which ultimately draw after them the whole protoplasmic body, or are themselves again drawn in, are distinguished as AMOEBOID MOVEMENTS. These movements resemble, externally, the motion of a drop of some viscous fluid on a surface to which it does not adhere, and are assumed to be due to surface tension, which the protoplasm can at different points increase or diminish by means of its quality of irritability.

By means of local changes of surface-tension, similar amoeboid movements are also exhibited by drops of lifeless fluids, such as drops of oil in soap solution, drops of an oily emulsion in water, or drops of mercury in 20 per cent solution of potassium nitrate in contact with crystals of potassium bichromate.

In the SWIMMING MOVEMENTS BY MEANS OF CILIA (125), on the other hand, the whole protoplasmic body is not involved, but it possesses special organs of motion in the form of whip-like FLAGELLA or CILIA. These, which are so delicate as to be difficult to see even with high magnifications, may be one, two, four, or more in number, and arranged in various ways (Figs. 218, 220). They extend through the cell-wall when this is present and move very rapidly in the water, imparting considerable velocity to the protoplast. The minute swarm-spores of *Fuligo varians* traverse 1 mm. (sixty times their own length) in a second, those of *Ulva* 0·15 mm., while others move more slowly. The *Vibrio* of Cholera, one of the most rapidly moving bacteria, takes 22 seconds to traverse a millimetre.

The cilia not only give rise to a forward movement, either in a straight or spiral line, but cause the whole organism to revolve around its longitudinal axis. In *Spirillum* it was found by METZNER that 40 revolutions of the cilia and 13 of the bacterium as a whole took place in each second. The details of the activity of cilia exhibit considerable variety. A swimming movement can be effected even by a simple oscillation of a curved cilium surrounded by a conical sheath. In other cases, however, the cilium has the form of a screw, which like the screw or propeller of a ship, determines by the direction of rotation a movement forwards or backwards. While the propeller is attached to an axis and moved by the rotation of the latter, the cilium, which is attached by its base to the organism, has to continually reproduce its screw-like shape during the movement. According to BÜTSCHLI this occurs by a spirally running line of maximum contraction continually moving round the cilium. It is not possible to enter further here into other and more complicated types of ciliary movement.

Diatoms exhibit a different class of movements. The Diatoms which have a slit or raphe in the siliceous cell-wall glide along, usually in a line with their longitudinal axis, and change the direction of their movements by oscillatory motions. From the manner in which small particles in their neighbourhood are set in motion, it is concluded that there exists a current of protoplasm, which extends to the outside through the raphe; this, according to O. MÜLLER, is the cause of the movement (126). The cells of Desmidiaceae effect their peculiar movements by local excretions of mucilage. The Oscillarieae appear to behave similarly (127).

In addition to such changes of place of whole cells there are also movements of the protoplasm within the cell-wall. Of these movements ROTATION and CIRCULATION (cf. p. 13) have to be distinguished.

In these movements the outermost layer of protoplasm in contact with the cell-wall remains at rest; the movement cannot thus be compared to that of an amoeba enclosed in a cell. The movement continues when the protoplasm has been detached from the cell-wall. Its cause must be looked for in changes of the surface-tensions between the protoplasm and the cell-sap.

B. The Conditions of Locomotion

Since these movements are due to protoplasm and its organs it will be readily understood that they depend on the general conditions for the life of the protoplasm. The existence and the activity of all these movements thus depend especially on a favourable temperature, and in aerobic plants (cf. p. 271) on the presence of free oxygen. The protoplasmic movement can, however, continue for weeks in the absence of oxygen in the case of facultative anaerobes like *Nitella*. Certain bacteria that are obligate anaerobes lose their motility on the entrance of oxygen; on the other hand, aerobic Bacteria which have ceased to move in the absence of oxygen resume their movement when a supply of this gas is available (p. 241). On overstepping the minimum or the maximum for these factors a loss of motility or a condition of rigor results. Thus we speak of cold-rigor, heat-rigor, etc. This condition can be removed by a return of the favourable conditions, but if it lasts long enough will ultimately lead to death.

In some cases it is sufficient that these general conditions of life should be present, but in others the movement only results on the application of special external stimuli.

FITTING has recently shown that the cells of *Vallisneria* exhibit no movements in pure water, but only when various substances are dissolved in it. By far the most effective among those substances which he investigated are the amino-acids. Even the slightest trace starts the movement, the threshold lying as deep as in the case of many animal hormones. One milligramme dissolved in 30-80 litres of water corresponds to this lower limit. This means that, if the calculation is based on the volume of an average sized cell of the mesophyll of *Vallisneria*, the one ten-billionth of a milligramme is effective (127a). Light also has a great influence on the movement of protoplasm. In cells of *Vallisneria*, which have become sufficiently accustomed to the dark, relatively small amounts of light will call forth protoplasmic movements. With an intensity of light amounting to 22·2 metre-candles the time of illumination need only be 80 seconds. Even a light of 0·5 metre-candle, if allowed to act for a sufficient time, will start the movement. It has been found that the movements of some bacteria are awakened by light, or by a sufficient concentration of the medium.

In giving a definite direction to movements of locomotion, external stimuli play a very special part. In the absence of such directive stimuli motile organisms move without a destination.

C. Tactic Movements

The main directive stimuli are one-sided illumination and dissolved substances unequally distributed through the water. The directive movements brought about by such factors are termed tactic; that effected by light is phototaxis, and that by dissolved substances chemotaxis. (Other tactic movements, see p. 333.)

The resulting movements bring the freely motile plant or the motile organ of a cell either towards or away from the stimulus; in the former case the taxis is positive, and in the latter negative. The nature of the reaction frequently depends not only on the object, but on the external conditions.

A distinction is made between TOPIC reactions in which, owing to local differences of the strength of the stimulus, the reacting organism orientates itself and moves in the direction of the effective stimulus, and PHOBIC reactions in which a variation in the strength or quality of the stimulus results in a movement which is against the stimulus but not in a definite direction.

1. Phototaxis (128)

Phototactic movements may be best observed when a glass vessel containing water in which are Volvocineae or swarm-spores of algae is exposed to one-sided illumination from a window. After a short time the uniform green tint of the water disappears, since the motile organisms have all accumulated at the better-illuminated side of the vessel. If the latter is turned through an angle of 180° the algae hasten to the side which is now illuminated. If, however, a stronger light, such as direct sunlight, is allowed to fall on the vessel the same organisms which till now have reacted positively become negatively phototactic and swim away from the source of light. Other external factors may have a similar effect.

In some organisms without chlorophyll, such as the plasmodia of the Myxomycetes, there is usually only a negative reaction, even to light of low intensity. There are also colourless organisms which have a positive phototactic reaction.

In the case of phototaxis both phobic and topic reactions are known. Certain bacteria especially react in a purely phobotactic manner, responding by a movement backwards to the change from light to darkness. They thus remain in an illuminated spot, since when their movement takes them into the dark they move back. Other phobotactic organisms, *e.g. Euglena*, often react in an apparently topotactic manner (pseudo-topotactic), since, owing to their morphological and physiological asymmetry, successive phobotactic reactions may lead to their placing themselves in the direction of the light. The purely topotactic organisms (*e.g. Volvox*), which, owing to localised differences in the strength of the stimulus in their bodies, move towards the direction of the stimulus, may also show apparently phobic reactions (pseudo-phobotactic reactions). This happens when the conditions of topotaxis, the local differences in strength of stimulus, are somewhat wanting, *e.g.* when a stimulus acts on all sides. Both pseudo-topotactic and purely topotactic organisms exhibit positive and negative phototaxis. If rays of light fall in various directions simultaneously on such organisms they move in the line of the resultant light. This "law of the resultant" holds not merely as regards direction but also as regards intensity.

Under experimental conditions with convergent light it is possible to induce negatively topotactic swarm-spores to move to brighter and brighter zones in increasing their distance from the source of light. But in Nature the phototactic movements of organisms doubtless lead them to positions of optimal brightness.

A very striking example of phototaxis is afforded by the chloroplasts, the mechanism of the movements of which is still quite unknown (^{129}). These movements have the result of bringing the chlorophyll-grain into such a position that it can obtain an optimal amount of light. This object is sometimes attained by rotation of the chloroplast, and sometimes by its movement to another position in the cell.

In the filamentous Alga *Mesocarpus*, the chloroplast has the form of a single plate suspended length-wise in each cylindrical cell. In light of moderate intensity they place themselves transversely to the source of light, so that they are fully illuminated (transverse position); when, on the other hand, they are exposed to direct sunlight, the chlorophyll plates are so turned that their edges are directed towards the source of light (profile position).

In the leaves of mosses and of the higher plants and in fern prothalli change in position of the numerous chloroplasts is effected by their movement in relation to the walls of the cells. In moderate light the chloroplasts are crowded along the walls which are at right angles to the direction of the rays of light (Fig. 274 *T*). They, however, quickly pass over to the walls parallel to the rays of light as soon as the light becomes too intense, and so retreat as far as possible from its action (Fig. 274 *S*). In darkness or in weak light the chloroplasts group themselves in still a third way (Fig. 274 *N*), determined by chemotactic influences from neighbouring cells.

In correspondence with the changes in the position of the chloroplasts, the colouring of green organs naturally becomes modified. In direct sunshine they appear lighter, in diffused light a darker green. The form of the chlorophyll-grains themselves undergoes modification during changes in their illumination; in moderate light they become flattened, while in light of greater intensity they are smaller and thicker.

2. Chemotaxis (^{130})

Chemotaxis results, as mentioned above, from the unequal distribution of substances dissolved in water. Positive chemotaxis leads to the irritable plants accumulating in the region of higher concentration of the chemotactic material.

Such substances are of definite nature. Thus, for example, many bacteria are "attracted" by particular organic or inorganic food-materials, *e.g.* peptone, sugar, meat-extract, phosphates, etc., while they are "repelled" by other substances such as acids and alkalies. While the chemotaxis here serves the process of nutrition, its use is different in the case of spermatozoids; these male sexual cells are thus attracted to the egg-cells. Fig 356 shows the chemotactic attraction of the spermatozoids by the female sexual cell of *Ectocarpus.* Nuclei and chloroplasts may also show chemotactic movements.

The positive chemotaxis of motile organisms has been demonstrated since the time of PFEFFER by mounting the chemotactically irritable organisms in water under a cover-glass, and introducing beneath this a capillary tube filled with the chemotactic substance. After a short time there is an accumulation of the chemotactic organisms in, and at the mouth of, the capillary tube.

Some of the organisms when they have entered the field of diffusion place themselves in the direction of the gradient and move directly towards the centre of diffusion (topic reaction). Others arrive by chance at the mouth of the capillary tube and are then prevented from moving away by a phobic reaction.

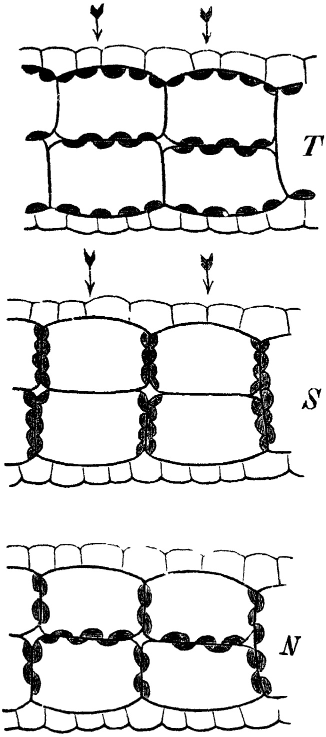


FIG 274.—Varying positions taken by the chlorophyll grains in the cells of *Lemna trisulca* in illumination of different intensity. *T*, in diffuse daylight, *S*, in direct sunlight, *N*, at night. The arrows indicate the direction of the light. (After STAHL.)

The spermatozoids of Ferns are attracted to the neck of the archegonium by malic acid or its salts, the same result comes about in the Lycopods from citric acid, in the Mosses from cane-sugar and in the Marchantiaceae from albumin. Frequently the most minute amounts of the substance are effective. Thus a 0.001% solution of malic acid is sufficient to attract the fern spermatozoids swimming in pure water. This minimal concentration of the chemotactic substance which determines by means of the capillary method a recognisable accumulation of the chemotactically sensitive organisms is termed the stimulus-threshold. The chemotactic movements only take place when the distribution of the chemotactically active substance is unequal and a diffusion gradient exists. But homogeneous solutions of the chemotactic substances are not without influence, for they diminish the sensibility of the organisms. By employing a homogeneous solution of the chemotactic substance the stimulus-threshold of the organism is raised; this follows a definite law. Thus in the case of the spermatozoids of ferns the following values were found by PFEFFER:

	Stimulus-threshold.
In water.	0·001% malic acid
,, 0·0005% malic acid . . .	0·015% ,, ,,
,, 0·001% ,, ,, ...	0·03% ,, ,,
,, 0·01% ,, ,, ...	0·3% ,, ,,

This shows that the same relation must always hold between the solution around the organisms and that acting chemotactically on them; the latter must be 30 times more concentrated than the former. This is known by the name of WEBER'S law and closely resembles the law of the same name in psycho-physics.

If chemotaxis is determined by oxygen it is called AEROTAXIS. It has been seen that bacteria which react in this way can be used to demonstrate the liberation of oxygen in carbon-assimilation (p. 241). In this case there is a positive aerotaxis of typical aerobionts, but on the other hand true anaerobionts exhibit a negative chemotaxis. Certain bacteria which are adapted to live at definite low pressures of oxygen can react to concentrations of this gas by positive or negative movements and thus seek out their optimal pressure of oxygen.

The phenomenon of HYDROTAXIS, a directive movement due to the unequal distribution of water-vapour in the air, may be associated with chemotaxis. A positive hydrotaxis is shown by the plasmodia of Myxomycetes, and this passes into negative hydrotaxis at the time of spore-formation.

There are many other tactic movements in addition to those that have been mentioned. OSMOTAXIS is the term employed when the assembling of motile organisms is brought about not by the chemical nature of a solution but simply by its concentration. In THERMOTAXIS it is the unequal distribution of heat, in GALVANOTAXIS the electric current, and in RHEOTAXIS water-currents which determine the movements of the organisms (130a).

II. MOVEMENTS OF CURVATURE

The **kinds of curvature** which may take place in the organs of attached plants are illustrated by Fig. 275. A four-angled prism is of equal length along each of its angles. If it is bent in one plane the angles of the concave side must become markedly shorter than those of the convex side. An elongation of one side or a shortening of the other side or simultaneous lengthening of one side and shortening of the opposite side must lead to curvature. When in this process of bending the column remains in one plane, it is spoken of simply as curved. When, however, it passes out of the one plane so that the bending follows a line oblique to the longitudinal axis it is spirally wound (*IV*). Lastly, when the column remains as a whole straight but its angles follow spiral lines, it is termed twisted (*III*). The torsion comes about by a difference in length between the middle line and the angles; all the latter are of equal length.

Ways in which Curvatures are produced.—In the production of curvatures we are always concerned, as has just been shown, with changes in the dimensions of an organ due to unequal lengthening or shortening. In bringing about these changes in dimension the following means are employed by the plant:

1. Growth. This can only lead to elongation.
2. Turgor-pressure. This can effect an elongation or a shortening according as it is increased or diminished.
3. Variations in the amount of water in the cell-wall or in dead cells. These also can effect either elongation or shortening.

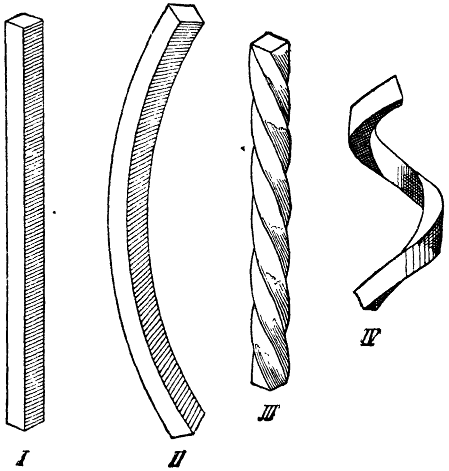


FIG. 275.—Four-angled prism. *I*, Straight; *II*, curved; *III*, twisted; *IV*, spirally wound.

According to the means employed in altering the dimensions, the curvatures of plants may be divided into GROWTH-CURVATURES, VARIATION MOVEMENTS DEPENDING ON TURGESCENCE, and HYGROSCOPIC MOVEMENTS. Since growth and turgor-pressure are vital phenomena, *i.e.* are essentially influenced by the living protoplasm, they will be treated below along with the locomotory movements which are dependent on the living substance of the plant. The hygroscopic movements, on the other hand, are not vital phenomena; they may occur in living organs, but equally well in dying or dead organs, and are brought about exclusively by external factors. The protoplasm only plays a part in these movements in that it has led to such a construction of the organs that changes in the amount of water present produce curvatures and not a simple change in length.

A. Hygroscopic Movements

Two quite distinct types of movement are included in the hygroscopic movements. In the first, which are termed IMBIBITION MECHANISMS (^{131}), the cell-walls increase in size on swelling or contract on shrinking.

The swelling depends on the fact that the water of imbibition is not contained in cavities like those in a porous body (such as a sponge or a piece of plaster of Paris) that contain the capillary water, but in being absorbed has to force apart the minute particles of the cell-wall. Conversely these particles approach one another again when the imbibition water evaporates and shrinking takes place. When on different sides of an organ there are cell-walls or layers of the wall which differ in their powers of imbibition, curvatures must take place every time the organ is moistened or dries. Though we are here dealing with purely physical phenomena, they may possess great importance for the plant.

The rupture of ripe seed-vessels, as well as their dehiscence by the opening of special apertures, is a consequence of the unequal contraction of the cell-walls due to desiccation. At the same time, by the sudden relaxation of the tension, the seeds are often shot out to a great distance (*Euphorbia*, *Geranium*, etc.). This dehiscence on drying is termed XEROCHASY, and is contrasted with the opening of the fruits and dispersal of the seeds in some desert plants when they are moistened (HYGROCHASY). The best example of this is the fruit of *Mesembryanthemum linguiforme.* The behaviour of the "Rose of Jericho" (*Anastatica hierochuntica*) is similar. The whole plant when fruiting dries up, and owing to the unequal shortening of the upper and under sides of the branches becomes contracted into a spherical mass. On the addition of water, the plant resumes its original form, its fruits open and shed the seeds which are thus under favourable conditions for germination. With *Anastatica* some other plants (*e.g.* *Odontospermum*) may be mentioned, to some of which the name Rose of Jericho is also applied. In certain fruits not only curvatures but torsions are produced as the result of changes in the amount of water they contain, *e.g.* *Erodium gruinum* (Fig. 276), *Stipa pennata*, *Avena sterilis* ; by means of these, the seeds bury themselves in the earth. If a partial fruit of *Erodium* having the form of Fig. 276 A is laid flat on the soil it starts a boring movement into the latter owing to differences in the water-content of the air. The obliquely backwardly directed hairs on the fruit lead to the movement being downwards into the ground.

The opening or closing of the moss sporogonium is, in like manner, due to the hygroscopic movements of the teeth of the peristome surrounding the mouth of the capsule. In the case of the Equisetaceae the outer walls of the spores themselves take the form of four arms, which, like elaters, are capable of active movements.

In order to call forth imbibition movements the actual presence of liquid water is not necessary, for the cell-walls have the power of absorbing moisture from the air. They are hygroscopic, and such structures as the fruit of *Erodium* are used to estimate the humidity of the air in hygrometers and weather-glasses.

The mechanisms which depend on the cohesive power of water are distinguished from those depending on imbibition. The COHESION MECHANISMS (182) were previously confounded with the latter, from which they differ in that, even during the movement, the cell-walls remain saturated with water. It is the lumen of the cell which diminishes in size when the loss of water, on which the movement depends, occurs. A good example is afforded by the movements of the sporangium of the Polypodiaceae on drying. The sporangia are stalked, biconvex bodies containing the spores within a wall composed of one layer of cells. While the rest of the wall is composed of thin-walled cells, one row of peculiarly thickened cells forms a vertically placed semicircle (Fig. 277 1 *a*). The cells of this ANNULUS (Fig. 277, 2) have their outer walls thin, the lateral walls increasingly thickened from the outside inwards, and the inner walls thick. On exposure to dry air the cells of the annulus gradually lose the contained water. The watery contents do not, however, separate from the cell-wall nor does a rupture occur in the liquid, since the adhesion to the wall and the cohesion of the molecules of water is very great, amounting to more than 300 atmospheres. A deformation of the cell-wall, therefore, follows the diminishing water-content; the thin outer wall (Fig. 277, 3) is pulled inwards, thus approximating the thickened lateral walls. There thus comes about an energetic one-sided shortening of the annulus which leads to the slow opening of the sporangium. The majority of the spores remain still attached to the sporangial wall. With further loss of water the contained water ultimately tears apart from the wall, and the cells of the annulus resume their original form. Since this occurs suddenly, the majority of the spores are forcibly thrown out, as the sporangium again closes. This catapult-like mechanism scatters the spores to a considerable

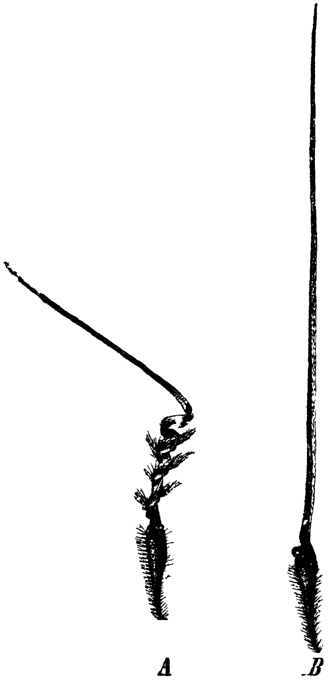


FIG. 276.—Partial fruit of *Erodium gruinum*. *A*, in the dry condition, coiled; *B*, moist and elongated. (After NOLL.)

distance and increases the chance of their finding suitable conditions for germination.

The sporangia of other Vascular Cryptogams and the walls of pollen-sacs afford in their opening other examples of cohesion-mechanisms. Many hygroscopic curvatures also depend on the co-operation of movements depending on imbibition and on cohesion.

B. Movements of Curvature in the Living Plant

As in the case of plants which exhibit active locomotion, the phenomena of movement in attached plants may occur when all the general conditions of vital phenomena are present, but sometimes only when a particular factor (stimulus) is acting. The latter determines either the amount of the curvature only or its direction also. Movements which take place without such specific external stimuli are termed AUTONOMIC, while the others are termed INDUCED or PARATONIC movements.

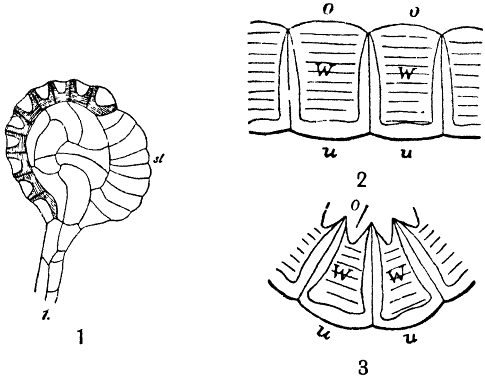


FIG 277.—1. Sporangium of a Polypodiaceous Fern. (After JOST.) 2. Cells of annulus in original position. 3. After partial evaporation of the water filling them (*w*); the upper cell-wall (*o*) is curved in, while the lower (*u*) retains its original length. (2, 3 after NOLL.)

1. Autonomic Movements of Curvature

The growth of the shoot or root in a straight line (with the characteristic grand period of growth, dependent, as has been shown, wholly on internal causes) is an autonomic movement. A number of growth-curvatures or nutations are associated with this growth, and it might almost be said that there is hardly such a thing as growth in a straight line. The tips of the organs describe extraordinarily irregular curves in space; they exhibit "circumnutations," as was discovered by DARWIN. While these curvatures are usually so slight as not to be perceptible without the aid of special methods, cases exist in which organs exhibit very conspicuous, striking, and regular autonomic growth-curvatures.

When the unequal growth is not confined to one side, but occurs alternately on different sides of an organ, the nutations which result seem even more remarkable. Such movements are particularly apparent in the flower-stalk of an Onion, which, although finally erect, in a half-grown state often curves over so that its tip touches the ground. This extreme curvature is not, however, of long duration, and the flower-stalk soon becomes erect again and bends in another direction.

If the line of greatest growth advances in a definite direction around the stem, the apex of the latter will exhibit similar rotatory movements (REVOLVING NUTATION). This form of nutation is especially marked in the tendrils and shoots of climbing plants, and facilitates their coming in contact with a support.

Among autonomic movements of curvature an important place is occupied by a number which are shown in the development of shoots, leaves and flowers. These have of late been specially investigated by GOEBEL who has given them the appropriate name of "unfolding movements."

The unfolding of most leaf and flower buds, for example, is a nutation movement which is induced by the more vigorous growth of the upper side of the young leaves (epinasty). The same unequal growth, in this case of the under side, manifests itself most noticeably in the unrolled leaves of Ferns and many Cycadeae (hyponasty). The stems of many seedlings are, on their emergence from the seeds, strongly curved, and this aids them in breaking through the soil ([133]).

Besides these nutations which result from growth, AUTONOMIC VARIATION MOVEMENTS are also met with, though less commonly. They are almost confined to foliage leaves, and indeed to those which have pulvini at the base of the petiole and of its further ramifications. Pulvini occur especially in Leguminosae and Oxalideae, also in *Marsilia*, and are characterised by a structure which corresponds to their particular function.

In the ordinary parenchymatous cell the cell-wall, owing to its growth in thickness, ceases to be stretched; on plasmolysis it therefore does not contract in the same degree in full-grown cells as it does in growing cells (cf. Fig. 233). Conversely on an increase of the internal pressure the wall only becomes slightly stretched. In some cases, however, and the pulvinus is an example, the cell-walls even in their fully-grown state are considerably distended by the turgor-pressure. This is shown not only by their behaviour on plasmolysis, but also by the persistence of marked tissue-tensions. A pulvinus of one of the Leguminosae, such as the Kidney Bean, has the vascular bundles and the sclerenchyma, which are peripherally arranged in the leaf-stalk (Fig. 278, 1), united to form a central and easily-bent strand; this is surrounded by a thick zone of parenchyma (Fig. 278, 2, 3). If the middle sheet of tissue is cut out from a pulvinus isolated by two transverse sections (Fig. 278, 4), the bulging of the cortical parenchyma both above and below shows the considerable tension. On splitting the portion of the pulvinus longitudinally as in Fig. 278, 5, the tendency towards expansion of the parenchyma, especially of its middle layers, is very clearly shown.

It will now be readily seen that an increase in turgescence on all sides will increase the tension between the vascular bundle and the parenchyma and thus increase the rigidity of the pulvinus. On the other hand, an increase of the turgor-pressure on one side or a diminution on the other side, or the occurrence of both these changes together, will cause a lengthening of the one side and a shortening of the other side which naturally curves the pulvinus. The vascular bundle is passively bent, and undergoes no alteration in length. The passive movement of the part of the leaf attached to the pulvinus is due to the curvature of the pulvinus.

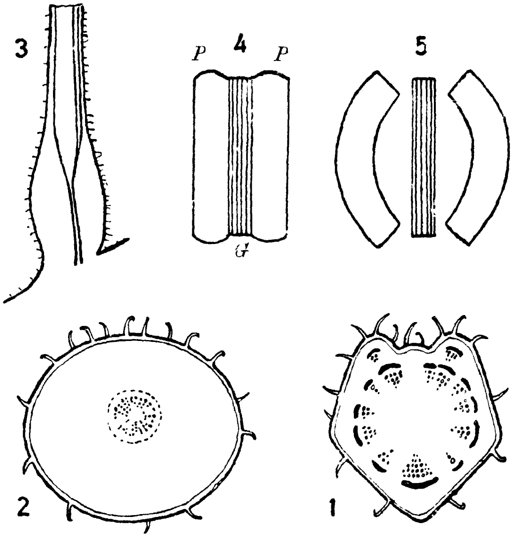


FIG. 278.—*1*, Transverse section through the petiole of the Bean. *2*, The same through the pulvinus. *3*, Longitudinal section through the pulvinus and its continuation into the petiole. *4*, Slice through middle of pulvinus placed in water; *P*, cortical parenchyma; *G*, vascular bundle. *5*, The same after separation of cortex from vascular bundle. (4 and 5 after SACHS. All slightly enlarged.)

Autonomic variation movements are probably present in all leaves provided with pulvini, but only attain a striking degree in a few plants.

Thus the small lateral leaflets of *Desmodium gyrans* move uniformly or move interruptedly in elongated ellipses. At higher temperatures (30-35° C.) the movement is very rapid, the course being completed in half a minute. The movement of the leaflets of *Oxalis hedysaroides* is still more rapid, the tip moving through 0·5-1·5 cm. in one or a few seconds. While the autonomic movements of these two plants do not appear to be affected by light, those of *Trifolium pratense* are completely suppressed in light. In the dark, however, the terminal leaflet exhibits oscillatory movements with an amplitude that may exceed 120° ; these are regularly repeated in periods of two to four hours.

As has been pointed out the external factors on which life is dependent (p. 202) must be present in sufficient degree for these curvatures to take place. Overstepping the maximum or the minimum for external factors leads to conditions of rigor in which no movements take place. Thus a condition of rigor due to cold, heat, darkness, dryness, etc., can be recognised. Injurious chemical influences (poisonous effects) also lead to a condition of rigor.

2. Paratonic Movements (Stimulus Movements) (134)

In the induced or paratonic movements an external factor always acts as a stimulus and starts the movement. By means of these movements attached organisms bring their organs into the positions in which their functions can be best carried out. If the organs of a seedling continued to grow on in the directions which have been accidentally brought about on sowing the seed, the root would often grow into the air and the shoot into the soil.

Light, heat, gravity, and chemical or mechanical influences of the most various kinds enable the plant to orientate itself in its environment. The different organs of a plant often show quite different reactions to the same external stimulus. Thus the stem and root, while both tending to place themselves in the direction of the rays of light, usually grow towards or away from its source respectively ; the leaves, on the other hand, place their flat surfaces at right angles to the incident rays. The mode of reaction is not determined once and for all, but can be profoundly modified. The tone of the plant is thus altered, the change being brought about by either internal or external factors.

Those movements which bring about a particular position with regard to the direction of action of the stimulus may be grouped together as MOVEMENTS OF ORIENTATION or TROPISMS. The other movements of curvature, leading to the assumptions of definite positions with respect to the plant and not to the direction of the stimulus, are termed NASTIC movements.

(a) Tropisms

In the movements of orientation we have to distinguish orthotropic (parallelotropic) and plagiotropic organs. The former place themselves in the direction of the stimulus and approach the source of the stimulus (positive reaction) or move away from it (negative reaction). Plagiotropous organs place themselves at right angles to the direction of the stimulus or obliquely to its direction. The mode of reaction of any particular organ may be changed by external or internal factors. The movements of orientation are distinguished as phototropic, geotropic, etc., according to the stimulus bringing them about.

The tropisms of attached plants correspond to the tactic movements of motile plants. As in the case of the latter, their significance lies in the attainment of favourable conditions of life. The effective stimulus, the positive and negative modes of reaction, and the alternation from one to the other are completely analogous to the phenomena already described in relation to tactic movements.

1. GEOTROPISM (135)

It is a matter of experience that the trunks in a Fir wood are all vertical, and therefore parallel to one another; the branches and leaves of those trees, on the other hand, take other positions. If, instead of a tree, we consider a seedling, for example of the Maize, we find that, at any rate to begin with, the organs stand in the vertical line. At the same time, we here observe more readily than in the case of a tree the totally different behaviour of the root and the stem, the former growing vertically downwards and the latter upwards. If we bring the seedling from its natural position and lay it horizontally we find that a curvature takes place in both organs; the root curves downwards, and the shoot of the seedling upwards. Since these curvatures are not effected at the region where the root passes into the shoot, but in the neighbourhood of the apices of the two organs, a region of variable length remains horizontal, and only the two ends of the plant are brought by the curvature back into their natural directions, and continue to grow in them. That this vertical growth of the main root and main stem is due to gravity is apparent from direct observation, which shows that these organs are similarly orientated all over the globe, and lie in the direction of radii of the earth. The only force acting everywhere in the direction of the earth's radius that we know of is gravity. Not, however, as a result of this line of thought, but from the experiments of KNIGHT (1806), was this knowledge introduced into our science. KNIGHT'S experiments rest on the following consideration. It is evident that gravity can only cause the root to grow downwards, and the stem to grow upwards, if the seed is at rest and remains in the same relative position to the attractive force of the earth. From this KNIGHT conjectured "that this influence could be removed by the constant and rapid change of position of the germinating seed, and that we should further be able to exert an opposite effect by means of centrifugal force." He therefore fastened a number of germinating seeds in all possible positions at the periphery of a wheel, so that the root on emerging would grow outwards, inwards, or to the side, and he caused the wheel to rotate round a horizontal axis. Since this rotation was very rapid, not only was the one-sided action of gravity excluded, but at the same time a considerable centrifugal force was produced, which in its turn influenced the seedlings. The result of the experiment was that all the roots grew radially away from, and all the shoots radially towards the centre of the wheel. Thus the centrifugal force determined the orientation of the seedlings as gravity does normally.

In another experiment KNIGHT allowed gravity and centrifugal force to act simultaneously but in different directions on the seedlings. The plants were fastened on a wheel which rotated round a vertical axis. When the distance of the plants from the centre and the rapidity of rotation were so adjusted that the mechanical effects of the centrifugal force and of gravity were equal, the roots grew outwards and downwards at an angle of 45° and the stem inwards and upwards at the same angle. As the rapidity of rotation increased, the axis of the seedlings took a position approximating more to the horizontal. It results from these experiments that the plant does not discriminate between gravity and centrifugal force, and that the one can be replaced by the other. Both these forces have this in common, that they impart to bodies an acceleration of mass. These facts are of the greatest importance for the experimental investigation of geotropism, since only the centrifugal force, and not the force of gravity can be varied in intensity in the laboratory.

An essential addition to the fundamental researches of KNIGHT was given much later (1874) by the experiments of SACHS. In these the plants were rotated round a horizontal axis as in KNIGHT'S first experiment, but the rotation was slow, taking ten to twenty minutes to effect one complete rotation. This is so slow that no appreciable centrifugal force is developed. Since, however, by the continual rotation any one-sided influence of gravity is eliminated, the roots and shoots grow indifferently in the directions which they had at the beginning of the experiment. In this experiment SACHS employed a piece of apparatus termed the KLINOSTAT.

The property of plants to take a definite position under the influence of terrestrial gravity is termed GEOTROPISM. It has been seen that there are not only orthotropic organs which place themselves in the direction of gravity, and grow positively geotropically (downwards) or negatively geotropically (upwards), but also plagiotropic organs which take up a horizontal or oblique position. The positions assumed by the lateral organs are also though as a rule not exclusively—determined by gravity.

All vertically upward-growing organs, whether stems, leaves (Liliiflorae), flower-stalks, parts of flowers, or roots (such as the respiratory roots of *Sonneratia* (Fig. 181), Palms, etc.), are negatively geotropic. When such negatively geotropic organs are forced out of their upright position, they assume it again if still capable of growth. In negatively geotropic organs, growth is accelerated on the side towards the earth; on the upper side it is retarded. In consequence of the unequal growth thus induced, the erection of the free-growing extremity is effected.

The actual course of the directive movement of geotropism, as will be seen from the adjoining figure (Fig. 279), does not consist merely of a simple, continuous curvature. The numbers 1-16 show diagrammatically, different stages in the geotropic erection of a seedling growing in semi-darkness and placed in a horizontal position (No. 1). The growth in the stem of the seedling is strongest just below the cotyledons, and gradually decreases towards the base. The curvature begins accordingly close to the cotyledons, and proceeds gradually down the stem until it reaches the lower, no longer elongating, portions. Owing to the downward movement of the curvature, and partly also to the after-effect of the original stimulus, the apical extremity becomes bent out of the perpendicular (Nos. 7, 8), and in this way a curvature in the opposite direction takes place. For two reasons this excessive curvature must again diminish (13-16); the stem is now exposed to another geotropic stimulus in the opposite direction to the first, and this is combined with a tendency to straighten, which is termed AUTOTROPISM (p. 359).

In some cases negatively geotropic curvatures may take place in full-grown (136) shoots, *i.e.* in such as no longer exhibit growth in length when not geotropically stimulated. Thus in woody stems and branches the growth in length of the cambium of the lower side may bring the organ into the erect position as a result of geotropism. The greater the resistance of the parts which have to be passively bent the more slow and incomplete will this response be. The so-called nodes of grasses, which in reality are leaf-cushions, can also be stimulated by geotropism to further growth. If the stimulus acts on all sides, as when the node is horizontally placed and rotated on the klinostat, all the parenchymatous cells exhibit a uniform elongation. If the node is simply placed horizontally the growth is limited to the lower side while the upper side is passively compressed (Fig. 280). By means of such curvatures in one or several nodes grass-haulms laid by the wind and rain are again brought into the erect position.

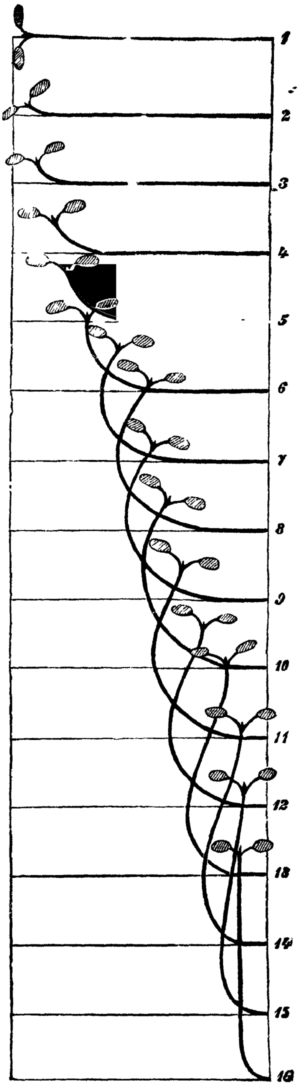


FIG. 279.—Different stages in the process of geotropic movement. The figures *1-16* indicate successive stages in the geotropic curvature of a seedling grown in semi-darkness: at *1*, placed horizontally; at *16*, vertical. For description of intermediate stages see text. (After NOLL. Diagrammatic.)

Positive geotropism is exhibited in

tap-roots, in many aerial roots, in the plumules of some Liliaceae and in the rhizome of *Yucca.* All these organs, when placed in any other position, assume a straight downward direction, and afterwards maintain it. Positively geotropic, like negatively geotropic, movements are possible only through growth. The power of a downward curving root-tip to penetrate mercury (specifically much the heavier), and to overcome the resistant pressure, much greater than its own weight, proves conclusively that positive geotropism is a manifestation of an active process. Positive geotropic curvature is due to the fact that the growth of an organ in length is promoted on the upper side, and retarded on the side turned towards the earth (137). Fig. 281 represents the course of the geotropic curvature in a root.

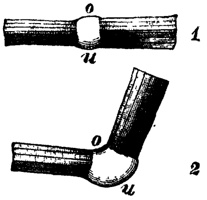


Fig. 280.—Geotropic erection of a grass-haulm by the curvature of a node. *1*, Placed horizontally, both sides (*u*, *o*) of the node being of equal length; *2*, the under side (*u*) lengthened, the upper side (o) somewhat shortened by compression; as a result of the curvature the grass-haulm has been raised through an angle of 75°. (After Noll.)

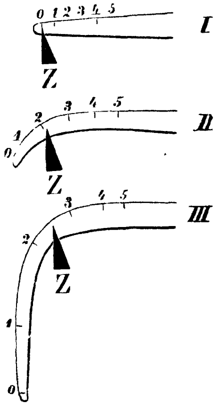


Fig. 281.—Geotropic curvature of the roots of a seedling of *Vicia Faba.* *I*, Placed horizontally; *II*, after seven hours; *III*, after twenty-three hours; *Z*, a fixed index. (After Sachs.)

Most lateral branches and roots of the first order are plagiogeotropic, while branches and roots of a higher order stand out from their parent organ in all directions. THESE ORGANS ARE ONLY IN A POSITION OF EQUILIBRIUM WHEN THEIR LONGITUDINAL AXES FORM A DEFINITE ANGLE WITH THE LINE OF THE ACTION OF GRAVITY. A special instance of plagiogeotropism is exhibited by strictly horizontal organs, such as rhizomes and stolons, which, once they have attained their proper depth, show a strictly TRANSVERSE GEOTROPISM (diageotropism). Should the proper depth not be attained, the plant tends towards it by upwardly or downwardly directed movements, and then takes on the horizontal growth The oblique position naturally assumed by many organs is in part the result of other influences (137a).

A special form of geotropic orientation is manifested by dorsiventral organs, *e.g.* foliage leaves, zygomorphic flowers (p. 69). All such dorsiventral organs, just as radial organs that are diageotropic, form a definite angle with the direction of gravity, but are only in equilibrium when the dorsal side is uppermost. It is immaterial which side of a radially symmetrical organ is uppermost so long as the axis of the organ has the correct inclination. In the orientation of dorsiventral organs, not merely simple curvatures but torsions are concerned. The rotation of the ovaries of many Orchidaceae, of the flowers of the Lobeliaceae, of the leaf-stalks on all hanging or oblique branches, of the reversed leaves (with the palisade parenchyma on the under side) of the Alstroemeriae and of *Allium ursinum*, all afford familiar examples of torsion regularly occurring in the process of orientation

The foliage leaves which possess pulvini must again be specially mentioned among dorsiventral organs, since they can change their position by geotropic variation movements in the fully-grown state.

Twining Plants (138), which are found in the most various families of plants, have shoots which require to grow erect but are unable to support their own weight. The utilisation of a support produced by the assimilatory activity of other plants is a peculiarity they possess in common with other climbers, such as tendril- and root-climbers. Unlike them, however, the stem-climbers accomplish their purpose, not by the help of lateral clinging organs, but by the capacity of their main stems to twine about a support. The first internodes of young stem-climbers, as developed from the subterranean organs which contain the reserve food-material, as a rule stand erect. With further growth the free end curves energetically to one side and assumes a more or less oblique or horizontal position. At the same time the inclined apex begins to revolve in circles like the hand of a watch (cf. p. 338). This movement continues from the time of its inception as long as the growth of the shoot lasts, and as a rule takes place in a definite direction. In the majority of twining plants the circling movement as seen from above is in the direction opposite to that of the hands of a watch (towards the left as we commonly express it). The Hop and the Honeysuckle twine to the right, in the direction of the hands of a watch. Either direction in different individual plants, and even a change of direction in the same individual, have been observed in *Polygonum Convolvulus* and *Loasa lateritia.*

The revolving movement is regarded by some authors as purely autonomic; on the other hand, it is held that gravity has a determining influence upon it. This disputable question is still unsettled.

The commencement of the revolving movement does not by itself determine a twining movement. This only begins when the shoot meets a more or less vertical and not too thick support. This is enclosed in loose and at first very horizontal spirals, which gradually become more erect and steeper. The plants that circle to the left are also left-handed climbers, *i.e.* the spiral which their stem forms (Fig. 282, 1), mounts from the left to the right and, as seen from above, against the direction of the hands of a watch. Similarly the plants that circle to the right are right-handed climbers (Fig. 282, 2). The straightening results from negative geotropism and leads under otherwise favourable conditions when the support is subsequently removed to a complete obliteration of the spiral coils, the straightened stem appearing twisted. If the support is not removed it leads to tightening of the spiral and increased pressure on the support. The twining movement thus comes about by the revolving movement together with negative geotropism. The support plays a part in that it prevents the otherwise inevitable straightening. It must stand more or less vertically, because otherwise it would not be continually grasped by the overhanging tip of the shoot.

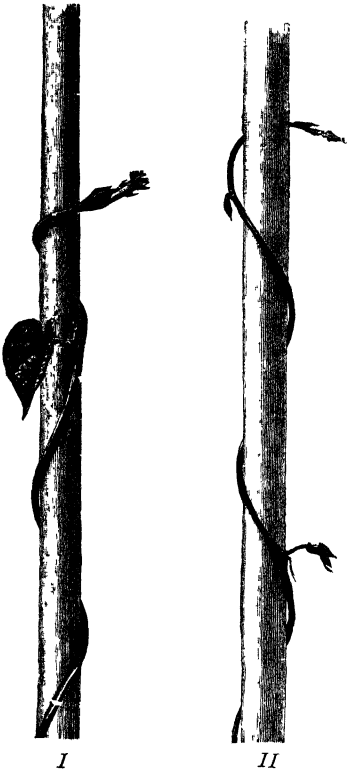


FIG. 282.—*I*, Sinistrorse shoot of *Pharbitis*. *II*, Dextrorse shoot of *Myrsiphyllum asparagoides*. (After NOLL.)

The twining is further assisted by the shoots of the twining plant having when young elongated internodes while the leaves remain small. In this respect these shoots resemble those of etiolated plants; the delayed unfolding of the leaves allows of the regular circling of the tip which might otherwise be interfered with by the leaves encountering the support. The firm hold on the support is frequently increased by the roughness of the surface of the stem owing to hairs, prickles, ridges, etc. Torsions also, the causes of which cannot be entered into here, have a similar effect.

Alteration of the Geotropic Position of Rest.—The position assumed by an organ as a result of a definite geotropic stimulation is not determined once and for all, but is liable to change owing to internal and external influences. There is thus a "change of tone" as regards geotropic stimulation. A certain "tone" is thus regarded as the normal one, and the resulting reactions are expressed in the distinction of orthotropous and plagiotropous, and positively and negatively geotropic organs respectively.

Among the external factors which influence the geotropic tone, light, temperature, oxygen, and gravity itself may be mentioned, and as an internal factor the developmental phase of the organ.

The alteration of geotropic reaction by the illumination has an important influence on the depth at which rhizomes occur. When the tip of a rhizome of *Adoxa* growing on a slope becomes exposed to the light, its transverse geotropism becomes altered to positive geotropism, and this leads to the rhizome again entering the soil. Frequently the influence of light on the parts of the plant above ground suffices to direct the subterranean rhizome. If the rhizome of *Polygonatum* is planted too high in the soil, although covered by earth and in the dark, the new growth turns obliquely downwards; if planted too deeply it turns upwards (Fig. 283). At the correct depth the rhizome is transversely geotropic. Light also acts strongly on the geotropism of lateral roots; when illuminated the lateral roots of the first order approach the orthotropous position more closely than they do in the dark.

An effect of temperature may be observed on the stems of some spring plants; these often lie on the ground at temperatures in the neighbourhood of 0° C. and only become orthotropous at higher temperatures. With lack of oxygen some roots and rhizomes become negatively geotropic, and thus reach regions where more oxygen is available.

Changes of tone due to internal causes are seen, for instance, in rhizomes, which at a certain stage of development change from the diageotropic position and become orthotropous, or in inflorescences which become positively geotropic after fertilisation (139). In this way the fruits of *Trifolium subterraneum* and of *Arachis hypogaea* become buried in the soil. In twining stems also a change of tone has been noted; while young they do not twine.

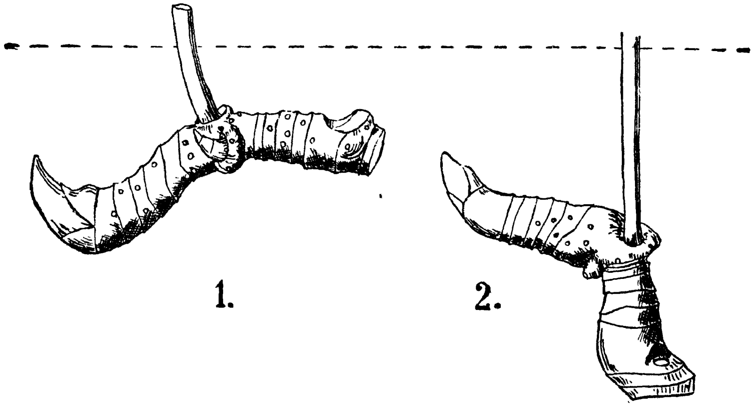


Fig. 283.—Rhizome of *Polygonatum*. The dotted line marks the surface of the soil. The aerial shoots are cut off. Rhizome 1 was planted too high; its continuation is downwards, only the terminal bud which will form a flowering shoot being directed upwards. Rhizome 2 was planted erect and too deep; its continuation is obliquely upwards. (After Raunkiaer.)

Geotropism as a Phenomenon of Irritability.—The discoverer of geotropism, Knight, attempted to explain the geotropic movements on purely mechanical lines; this did not seem difficult, especially for positively geotropic organs. He regarded them as simply following the attractive force of gravity till a condition of rest is attained. Later Hofmeister advanced similar views. The correct assumption, that we are concerned with complicated stimulus mechanisms in which terrestrial gravity only plays the part of the liberating factor, depends on the work especially of Dutrochet, Frank, and Sachs. Even the single fact that the root can carry out its geotropic curvature against the resistance of mercury is sufficient to call in question every purely mechanical explanation.

Only in recent times has the attempt been made to determine what is the primary effect of gravity in the plant (140). There is no doubt that we are concerned with an effect of pressure; the fact that gravity can be replaced by centrifugal force is in favour of this. This effect of pressure only comes into action in the case of orthotropous organs in proportion as it acts at right angles to the longitudinal axis, and thus in relation to the vertical component when the organ is placed obliquely. Since the value of this is determined by the sine of the incident angle, this is termed the SINE-LAW. Two forces, such as gravity and centrifugal force, acting at an angle behave according to the parallelogram of forces in producing their resultant effect (LAW OF THE RESULTANT). Lastly, it is clear that the pressure must act within the cells, and is in no way replaceable by external influences.

F. NOLL first elaborated the idea that there must be some bodies in the cells of greater specific gravity than the surrounding protoplasm, and capable, under the influence of gravity, of exerting a one-sided pressure on the protoplasm: On this taking place the protoplasm directs the processes of growth in accordance with the direction of the force of gravity. NĚMEC and HABERLANDT then suggested that these specifically heavier bodies (statoliths) might be found in certain starch-grains which show relatively rapid movements of falling in the cells. They found such starch-grains in the endodermis of the stem (p. 90) and in the cells of the root-cap. They assume that the stimulus of gravity can only directly affect portions of the plant provided with such starch-grains, but that it may be conducted from these points to others. It has in fact been demonstrated that in the root it is mainly the tip which receives the stimulus of gravity. According to investigations of STAHL and ZOLLIKOFER, it is possible in some cases to bring about the solution of the statolith starch; geotropism then disappears while growth and the capacity for phototropic response continues. This shows that in these cases the starch-grains are essential for the reception of the stimulus. According to other investigators it is not only such large constituents of the cell that are concerned in the process but also the microsomes, if these differ in specific weight from the hyaloplasm. This assumption would explain cases (*e.g.* moss-rhizoids) in which geo-perception is still possible after the disappearance of the starch. In geotropic fungi, where large statoliths are never found, other bodies must be effective.

The result of the primary pressure-effect was first supposed to be some chemical change; later, processes of imbibition and contraction were considered. More recently the suggestion has been entertained that the statoliths may not act by the pressure they bring about, but by altering the electric charges during their fall. If the starch-grains or the microsomes are negatively charged, their change of position would give rise to a difference of potential. Once this were present a movement of ions in the cell would result which would lead to shifting of the electrolytes of the protoplasm. In this way asymmetrical phenomena of imbibition might commence and thus lead to the curvature constituting the reaction (141).

As a rule we can only infer the geotropic irritability of an organ from the curvatures that take place, but in some cases it can be done independently of this reaction. Thus, for example, in some grass seedlings (Paniceae) that have a well-developed internode beneath the sheathing leaf, the latter becomes full-grown and no longer capable of curvature; it is, however, still geotropically sensitive, since on the sheath being exposed to the one-sided action of gravity the internode below, which is not itself sensitive to the stimulus, becomes curved. The geotropic stimulus must have been conducted from the sheathing leaf to the internode. In other grass seedlings (Poaeoideae) it has been observed that the tip of the sheath is much more sensitive to the geotropic stimulus than the zone of maximal growth, and a similar diminution of the sensibility on passing backwards from the tip holds for roots. It is possible with special apparatus to stimulate geotropically in opposite directions the apex and growing zone of such objects by centrifugal force, and to show that the curvature of the growing zone is then determined by the stimulated tip. There is thus a conduction of the stimulus in the basal direction which overcomes the direct stimulation of the growing zone. In such cases a clear separation of three processes is evident, the RECEPTION OF THE STIMULUS (PERCEPTION), the CONDUCTION OF THE STIMULUS, and the RESPONSE or REACTION. An organ may be perceptive without being able to react, or conversely. We are justified in assuming that these three parts of the process must be distinguished in cases where they are not so evident.

It can be inferred from these experiments that the degree of geotropic curvature and the rapidity with which it is produced in no way measures the amount of the stimulus, since they are largely dependent on the capacity for growth. The degree of geotropic stimulation depends both on the specific receptivity of the stimulated organ and on the amount of stimulus which it has received. For any given organ it is directly proportional to the amount of stimulus. By this is understood the product of the intensity of the stimulus and the duration of its action. Thus, it is the same so far as result is concerned, whether a high centrifugal force for a short time or a less force for a correspondingly longer time be employed. This law of the amount of stimulus ([142]) which stands in close relation to the laws of the sine, and of the resultant previously distinguished, only holds within certain limits.

It has been shown that an orthotropous organ, when laid horizontally under constant external conditions, begins to curve after a definite time. The period from the commencement of stimulation to the commencement of the reaction is termed the REACTION-TIME. To obtain a geotropic reaction, however, it is not necessary to stimulate an organ during the whole reaction-time. A much shorter period of stimulation is sufficient to obtain a geotropic curvature as an after-effect from the organ which has been replaced in the vertical position. The minimal period of stimulation after which a visible curvature results is termed the PRESENTATION-TIME. The law of amount of stimulus only applies to stimuli which last as long or somewhat longer than the presentation-time; the presentation-time is thus inversely proportional to the intensity of the stimulus. No corresponding increase of geotropic curvature follows larger amounts of stimulus.

As in the case of other properties of the plant the reaction-time and the presentation-time exhibit profound variations, so that typical variation curves are obtained by statistical investigation. TRÖNDLE found as mean reaction-times, 32 minutes for shoots of Oats, and 21 minutes for roots of Cress. Some seedlings of Oats reacted after less than 14 minutes while others required more than 49 minutes. In the majority of plants the reaction-times are longer. The presentation-times have been frequently found to be 2, 3, to 10 or more minutes.

Stimuli below the presentation-time are not without effect. On repetition (intermittent stimulation) they are summed up and result in a curvature when the sum of separate stimuli amounts to the presentation-time, if the intervals between the separate stimuli have not been too great. A lower limit for the duration of separate stimuli has not as yet been determined.

2. PHOTOTROPISM (HELIOTROPISM) (143)

Phototropic curvatures result from the incidence of light from one side. A good opportunity for the observation of heliotropic phenomena is afforded by ordinary window-plants. The stems of such plants do not grow erect as in the open, but are inclined towards the window, and the leaves are all turned towards the light. The leaf-stalks and stems are accordingly ORTHOTROPIC and POSITIVELY PHOTOTROPIC. In contrast to these organs the leaf-blades take up a position at right angles to the rays of light in order to receive as much light as possible. They are DIAPHOTOTROPIC, or TRANSVERSELY PHOTOTROPIC, in the strictest sense. It is less easy to observe examples of negative phototropism in which the organ grows away from the source of light. In Fig. 284 the phototropic curvatures which take place in a water culture of a seedling of the White Mustard are represented.

Sensitiveness to phototropic influences is prevalent throughout the vegetable kingdom. Even organs like many roots, which are never, under ordinary circumstances, exposed to the light, often exhibit phototropic irritability. Positive phototropism is the rule with aerial vegetative axes. Negative phototropism is much less frequent; it is observed in aerial roots, and sometimes also in climbing roots (*Ficus stipulata*, *Begonia scandens*), in the hypocotyl of germinating Mistletoe, in many, but not all, earth roots (*Sinapis*, *Helianthus*), in tendrils (chiefly in those with attaching discs), and in the stems of some climbers. By means of their negative heliotropic character, the organs for climbing and attachment, and the primary root of the Mistletoe, turn from the light towards, and are pressed firmly against, their darker supports.

For more exact investigation of phototropic movements it is necessary to be able to control more accurately the source and direction of the light. This can be accomplished by placing the plants in a room or box, lighted from only one side by means of a narrow opening or by an artificial light. It then becomes apparent that the DIRECTION of the incident rays of light determines the phototropic position; every alteration in the direction of the rays produces a change in the position of the phototropic organs. The apical ends of many positively heliotropic organs will be found to take up the same direction as that of the rays of light.

The exactness with which this is done is illustrated by an experiment made with *Pilobolus crystallinus* (Fig. 285). The sporangiophores of this fungus are quickly produced on moist horse- or cow-dung. They are positively phototropic, and turn their black sporangia towards the source of light. When ripe these sporangia are shot away from the plant, and will be found thickly clustered about the centre of the glass over a small aperture through which alone the light has been admitted; a proof that the sporangiophores were all previously pointed exactly in that direction.

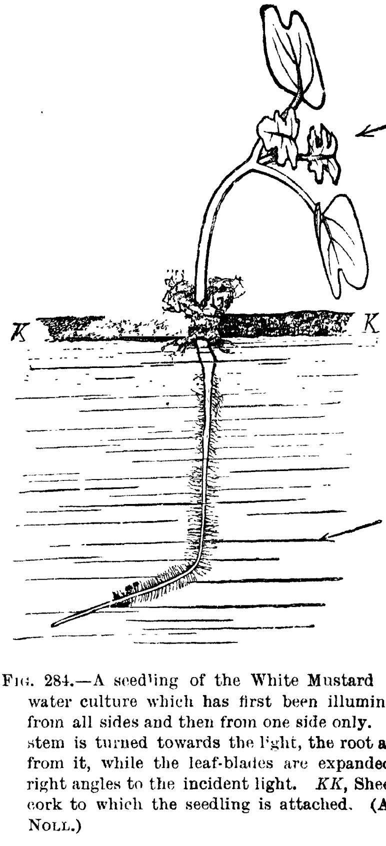


FIG. 284.—A seedling of the White Mustard in a water culture which has first been illuminated from all sides and then from one side only. The stem is turned towards the light, the root away from it, while the leaf-blades are expanded at right angles to the incident light. *KK*, Sheet of cork to which the seedling is attached. (After NOLL.)

The positive phototropic curvatures are brought about by THE SIDE TURNED TOWARDS THE LIGHT GROWING MORE SLOWLY, AND THAT AWAY FROM THE LIGHT MORE ACTIVELY, THAN UNDER ILLUMINATION FROM ALL SIDES. The converse distribution of growth is found in negative phototropism. As a rule CURVATURES ONLY TAKE PLACE IN THE REGION WHICH IS STILL IN A GROWING CONDITION, THE SHARPEST CURVATURE BEING AT THE REGION OF MOST ACTIVE GROWTH.

The course of phototropic curvature shows a complete correspondence with geotropic curvature (p. 343). It was formerly held that the increased growth of the shaded side in positive phototropism was produced by the beginning of etiolation, and that the diminished growth on the illuminated side was due to the retarding effect which light exerts upon growth in length. This view, which had for some time been abandoned, has recently been revived in a modified form by BLAAUW (144). According to him the phototropic curvatures depend on changes in growth in length due to the unequal illumination of the sides of the orthotropous organ which are directed respectively towards or away from the light. While in simple cases a close parallelism can be traced between the reaction of growth to light and the phototropism, there are other observations which cannot be accounted for by BLAAUW's theory in its present form.

In particular cases (145), phototropic curvatures have been demonstrated in organs which have finished their growth in length. This applies to perennial trees in which the cambium is probably concerned in the production of the curvatures. In nodes, such as those of the Gramineae and Commelinaceae, growth may be resumed under the influence of light, either by itself or associated with the effect of gravity.

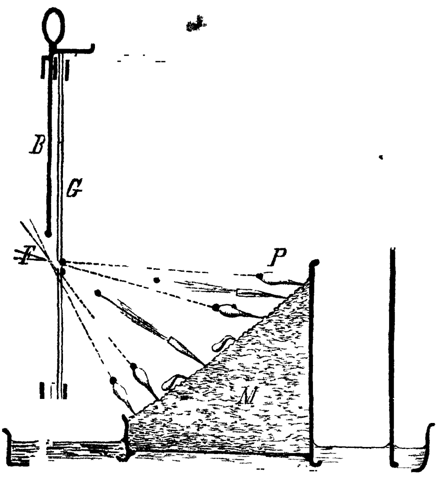


FIG. 285.—*Pilobolus crystallinus* (*P*), abjecting its sporangia towards the light. *G*, Sheet of glass; *B*, opaque case with a circular opening at *F*; *M*, vessel containing horse-dung. (Cf. description in text. After NOLL.)

If an organ has placed itself by a phototropic curvature in the direction of the incident light, it is equally illuminated on all sides, and in its phototropic resting position. If, without altering the direction or the intensity of the illumination, the plant is kept in constant rotation, around a vertical axis, by means of a klinostat, the phototropic stimuli acting on the different sides of orthotropous organs neutralise one another and no curvature takes place.

SACHS developed the theory that it is the direction of the light that is important in phototropism, as it is the direction of the force of gravity in the case of geotropism. More recently a different view has been generally taken, viz., that the phototropic stimulation depends on the unequal brightness of illumination of the different parts of the sensitive organ (146).

A definite decision on this question is not possible on our present knowledge. The critical question is whether an organ is to be regarded as reacting as a whole to the stimulus of light, or whether the parts of an organ or of a cell individually perceive the stimulus. In the former case only the direction of the light in the organ would be responsible for the reaction; in the second case the direction of the light only comes into play by determining the different intensities of illumination of the different cells or parts of a cell; the reaction itself would be determined by these secondary differences of intensity. Recent researches have clearly shown, in contrast to earlier views, that even in multicellular organs the direction of the light in the case of one-sided illumination plays the main part, as it does in the illumination of the single cell.

TRANSVERSE PHOTOTROPISM is confined almost entirely to leaves and leaf-like assimilatory organs, such as fern prothallia and the thalli of Liverworts and Algae. In these organs transverse phototropism predominates over all other motory stimuli. Such organs become placed at right angles to the brightest rays of light to which they are exposed during their development; in this process torsions of the leaves or internodes are combined with the simple curvatures.

In very bright light the transverse position of the leaves may become changed to a position more or less in a line with the direction of the more intense light rays. In assuming a more perpendicular position to avoid the direct rays of the midday sun, the leaf-blades of *Lactuca Scariola* and the North American *Silphium laciniatum* and the leaf-like shoots of some Cacti take the direction of north and south, and so are often referred to as COMPASS PLANTS. The foliage leaf has thus, like the chloroplast of *Mesocarpus*, the power of assuming either a profile or a full-face position, and thus regulating the amount of light received.

A number of foliage leaves possess pulvini (Figs. 131, 278) at the base of the petiole, and also at the bases of secondary and tertiary branchings; variation movements are effected by the aid of these. In this way these leaves are able to change their position throughout life, and at any moment to assume the position which affords them the optimal supply of light. They do not have a fixed light-position determined by the strongest illumination during their development, but they sometimes expose their edges and sometimes their surface to the light (147).

Phototropic curvatures can be effected in light of all the wave-lengths of the visible spectrum. The blue and violet rays, just as they are more effective phototactically, have a greater phototropic effect than other rays of the same energy-value.

ALTERATION OF TONE (148).—A particular part of a plant does not always react in the same way to one and the same stimulus; the mode of reaction may be altered by age or external influences. In this sense the terms "tone" and "change of tone" are used.

The flower-stalks of *Linaria cymbalaria* are at first positively phototropic. After pollination, however, they become negatively phototropic, and as they elongate they push their fruits into the crevices of the walls and rocks on which the plant grows (p. 282).

Among external factors that alter the tone the amount of illumination itself is particularly important. Small amounts of light falling from one side on *Avena* produce without exception a positive phototropic curvature; larger amounts give a weaker positive soon followed by a negative curvature; still larger amounts give a purely negative reaction. With further increase in the illumination a positive reaction is again obtained, and later a weakened positive if not a negative reaction. How far the intensity of the illumination also influences the results cannot be discussed here.

Phototropism, like geotropism, is a PHENOMENON OF IRRITABILITY (149). In it the perception and conduction of the stimulus and the reaction or response to it can also be distinguished; there are also presentation-time and reaction-time. Further, the law of amount of stimulus holds within narrow limits. A further law, which, though only a special case of the law of amount of stimulus, is of interest because first recognised for light-perception by the human eye, is known as TALBOT'S law (150). This states that stimuli due to one-sided illumination which individually are below the threshold can be added together, and that the sum of the separate stimuli has exactly the same effect as if they had acted as a single stimulus at one time. The separate stimuli must not be separated by too long intervals of darkness, for otherwise the effect of the one stimulus has died out before the second stimulus acts.

Localisation of Phototropic Stimulation.—Often the stimulus of light is received at the same place that the movement is effected. In certain leaves, however, the lamina is able to perceive a phototropic stimulus without being able to carry out the corresponding movement; this takes place only after the stimulus has been conducted to the leaf-stalk. It is true that the leaf-stalk can also react to direct stimulation, but as a rule the dominant impulse proceeds from the lamina. Still more striking relations are met with in the seedlings of certain Grasses; in some Paniceae only the tip of the so-called cotyledon can be phototropically stimulated, and only the hypocotyledonary segment of the stem, separated by some distance from the tip of the cotyledon, is capable of curvature. In this case there is a well-marked distinction between a perceptive organ and a motile organ; the similarity to corresponding phenomena in geotropism and in the animal kingdom is very striking. There is an essential difference, however, in the method of transmission of the stimulus (151); "Nerves" are completely wanting in the plant, and the stimulus is conveyed from cell to cell. This can still take place after the organic connection is interrupted by a cut if the interval is filled up with gelatine. On the other hand, if a layer of tin-foil is inserted all conduction ceases. If the tip of a Grass seedling is cut off and then replaced on the stump the stimulus of light received by the tip can be conducted across the wound to the basal region; the experiment succeeds even if the tip from another species of Grass is placed on the stump. It is clear from this that some diffusible substance must be concerned in the conduction of the stimulus.

This substance which must be thought of as a growth hormone is probably produced in the outermost cells of the tip and, under the conditions of darkness or uniform illumination, diffuses uniformly downwards. If such a seedling is illuminated from one side various things may occur. By a diminution of permeability the cells of the anterior side may become less effective than those of the side farther from the light. It may be, however, that the growth-hormone is destroyed by the stronger light acting on the cells of the anterior side. Lastly it might be supposed that the light caused a displacement of the material from the anterior to the posterior side. There is still uncertainty as to which of these possibilities is realised (152).

3. CHEMOTROPISM (153)

Those directive movements which are brought about by the unequal distribution of dissolved or gaseous substances in the neighbourhood of the plant are termed chemotropic. In the case of fungi and of pollen-tubes, chemotropic movements have been demonstrated which bring the organism into a certain optimal concentration of particular substances. With the same organism and the same stimulating substance these movements are sometimes positive and sometimes negative; positive when they lead towards a higher concentration of the substance, and negative in the converse case. In the case of pollen-tubes sugar and proteins are the chief substances that act as stimuli; in fungi, in addition to sugar, peptone, asparagin, compounds of ammonia and phosphates. There are also substances such as free acids which always have a repellent influence even in extremely weak concentration. This also holds as regards the fungi for metabolic products of unknown nature that diffuse out of the cells. Chemotropic irritability has also been demonstrated in roots, though it cannot be said that it plays an important rôle in their life.

In the examples of chemotropism given above, the stimulating substances were solid substances in solution. When, on the other hand, the plant is induced to perform directive movements by the unequal distribution in a space of aqueous vapour or gases, a distinct name has been required, though no distinction of principle can be drawn. Irritable movements caused by differences in moisture are termed HYDROTROPIC, while those brought about by gaseous differences are termed AEROTROPIC. Aerotropism has been proved for pollen-tubes, roots, and shoots, and hydrotropism for roots and moulds. Thus roots are positively hydrotropic and seek out the damper spots in the soil by reason of this irritability. The sporangiophores of the Mucorineae are negatively hydrotropic and thus grow out from the substratum. These reactions may be so energetic as to overcome other (*e.g.* geotropic) stimuli.

4. TRAUMATROPISM (154)

Wounding a part of a plant on one side may lead to an arrest of growth in the neighbourhood of the wound, so that this side becomes concave. This, however, is not a tropistic curvature in response to a stimulus. By TRAUMATROPISM is understood a very different phenomenon, which is most readily observed in roots. If the growing point of a root is cut, or burnt, or corroded on one side, a curvature occurs at some distance from it in the growing zone. This curvature is termed negatively traumatropic, since by it the tip of the root is turned away from the injurious agency. The region of the growing zone vertically above the wound grows more actively than the opposite side. The special interest of this tropism lies in the clear distinction between the place of reception of the stimulus and the place of the reaction; a well-marked conduction of the stimulus is thus demonstrated.

Negative traumatotropism is also occasionally shown by the above-ground organs, but usually these show a positive reaction. That this is not a mechanical result of the one-sided arrest of growth caused by the wound, but a true stimulus-movement is shown by the frequent acceleration of growth above the mean rate, and by the conduction of the stimulus to a considerable distance.

5. HAPTOTROPISM (THIGMOTROPISM) (155)

A curvature inwards on one-sided contact is found especially in tendril-climbers (p. 172) which seek by such grasping movements to encircle the touching body and utilise it as a support. The arrangement thus resembles what was seen in the case of twining plants, but the movements are not in any sense geotropic. In the case of tendril-climbers, the attachment to the support is effected, not by the main axis of the plant, but by lateral organs of various morphological character (cf. p. 172). These may either retain, at the same time, their normal character and functions (as foliage leaves, shoots, or inflorescences), or, as is usually the case, become modified into typical tendrils and serve solely as climbing organs. Contact with a solid body quickly induces an increase in the growth, greatest immediately opposite the point of contact and gradually diminishing till this is reached so that even in the middle line the effect is considerable. Thus the touched side of the tendril becomes concave, which leads to it coiling about the support. The more slender the tendrils and the stronger their growth, the more easily and quickly this process occurs. Some tendrils grasp their supports very quickly (*Passiflora*, *Sicyos*, *Bryonia*), while others are very slow (*Smilax*, *Vitis*). Owing to the tendency of the curvature to press the tendrils more and more firmly against the support, deep impressions are often made by them upon yielding bodies, soft stems, etc

According to PFEFFER'S investigations, it is of great importance to the tendrils in the performance of their functions that they are not induced to coil by every touch, but only through CONTACT WITH THE UNEVEN SURFACE OF SOLID BODIES. Rain-drops consequently never act as a contact-stimulus; even the shock of a continued fall of mercury produces no stimulation, while a fibre of cotton-wool weighing 0·00025 mgr. is sufficient to stimulate the tendril.

Probably the so-called tactile pits (Figs. 286, 287) favour the reception of such weak stimuli. These are pits in the outer epidermal walls which widen outwards and are filled with protoplasm. They are found, for instance, in the Cucurbitaceae, but may be wanting from some very irritable tendrils (*e.g.* in *Passiflora*). Some tendrils that are only sensitive on one side have the tactile pits correspondingly localised. On the whole tendrils are more or less dorsiventral, and their reactions are thus frequently rather nastic than tropistic.

The tendrils of some plants (*Cobaea*, *Eccremocarpus*, *Cissus*) are irritable and capable of curving on all sides; others (tendrils of Cucurbitaceae, etc., with hooked tips) are, according to FITTING, sensitive on all sides but only curve when the under side is touched; if the upper surface is at the same time stimulated, curvature is arrested.

In the more typically developed tendrils the curvature does not remain restricted to the portions directly subjected to the action of the contact-stimulus. Apart from the fact that, in the act of coiling, new portions of the tendril are being continually brought into contact with the support and so acted upon by the stimulus, the stimulation to curvature is also transferred to the portions of the tendril not in contact with the support. The first result of this is that the tip of the tendril becomes coiled round the support. Later the portion between the support and the parent-shoot becomes coiled, just as occurs in time with tendrils that have not grasped a support. While, however, in the latter case a single spiral results, the basal part of a tendril that has become attached must form at least two spirals in opposite directions, separated by a POINT OF REVERSAL (Fig. 288 *x*). By the spiral coiling of the tendrils the parent-stem is not only drawn closer to the support, but the tendrils themselves acquire greater elasticity and are enabled to withstand the injurious effects of a sudden shock.

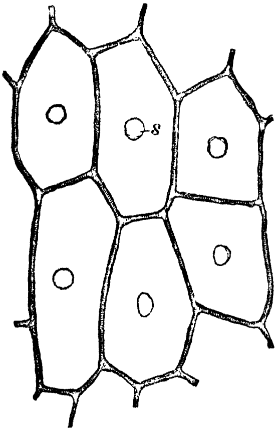


FIG. 286.—Surface view of cells from the sensitive side of the tendril of *Cucurbita Pepo*, showing tactile pits, *s*. (× 540. After STRASBURGER.)

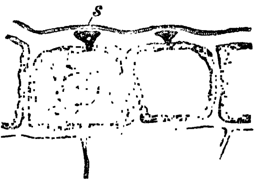


FIG. 287.—Transverse section through similar cells to those in Fig. 68; a small crystal of calcium oxalate (*s*) is present in the tactile pit. (× 450. After STRASBURGER.)

Advantageous changes also take place in the anatomical structure of the tendrils after they are fastened to the supports. The young tendrils, during their rapid elongation, which under favourable conditions may amount to 90 per cent of their length, exhibit active nutations, and thus the probability of their finding a support is enhanced. During this time they remain soft and flexible, while the turgor rigidity of their apices is maintained only by collenchyma. In this condition they are easily ruptured, and have but little sustaining capacity. As soon, however, as a support is grasped, the coiled-up portion of the tendril thickens and hardens, while the other part lignifies and becomes so strengthened by sclerenchymatous formations that the tendril can finally sustain a strain of several pounds. When the tendrils do not find a support they usually dry up and fall off, but in some cases they first coil themselves into a spiral.

Tendril-climbers are not, like twining plants, restricted to nearly vertical supports, although, on account of the manner in which the tendrils coil, they can grasp only slender supports. A few tendril-climbers are even able to attach themselves to smooth walls. Their tendrils are then negatively phototropic, and provided at their apices with small cushion-like outgrowths, which may either develop independently on the young tendrils, or are first called forth by the stimulus of contact. These cushions become fastened to the wall by their sticky excretions and then grow into disc-like suckers, the cells of which come into such close contact with the support that it is easier to break the lignified tendrils than to separate the holdfasts from the wall. Fig. 203 represents the tendrils of *Parthenocissus tricuspidata.* The suckers occur on its young tendrils in the form of knobs. In other species of Wild Vine the suckers are only produced as the result of contact, and the tendrils of these plants are also able to grasp thin supports.

Sometimes, as in the case of *Maurandia scandens* (Fig. 289), the leaf-stalks, although bearing normal leaf-blades, are irritable to contact-stimuli and behave as tendrils. Of leaf-stalks which thus act as tendrils, good examples are afforded by *Tropaeolum*, *Solanum jasminoides*, *Nepenthes*, etc. In other cases the midribs of the leaf-blades themselves become prolonged and assume the function of tendrils (*Gloriosa*, *Littonia*, *Flagellaria*). In many species of *Fumaria* and *Corydalis*, in addition to the leaf-stalks, even the stalks of the leaflets twine around slender supports, while the parasitic shoots of *Cuscuta* (Fig. 214) are adapted for both twining and climbing. In some tropical plants axillary shoots are transformed into tendril-like climbing hooks. Climbing parts of the thallus occur in some Thallophyta (Florideae).

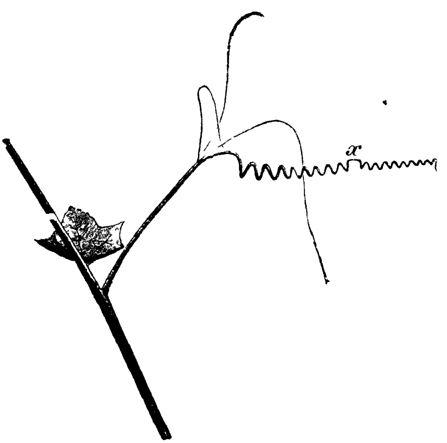


FIG. 288.—Portion of a stem of *Sicyos angulatus*, one of the Cucurbitaceae, with tendril. The branch-tendril has grasped the upright support on the right and the free portion has become spirally wound. *x*, Point of reversal in the coiling of the tendril. (After NOLL.)

Haptotropism is widespread among plants. Etiolated seedlings are always somewhat haptotropic, and this holds frequently for older shoots of green plants, especially of twining and climbing plants. The sensitiveness in these cases differs from that of tendrils in being excited by any contact, *e.g.* of falling water drops. No use appears to attach to this power (156).

STARK showed that in the haptotropism of seedlings the law of the resultant holds. He further showed that WEBER's law also applies. Thus if opposite flanks are stimulated unequally the curvature depends on the relation between the amounts of stimulus. Further, if the two opposite sides are stimulated equally strongly and a stimulus from one side is allowed to act in a plane at right angles, WEBER's law holds (157).

While a number of tropisms have been dealt with, this by no means exhausts the known cases. **Thermotropism**, in which heat is the stimulus, **rheotropism**, concerned with moving water, and **galvanotropism**, may be mentioned, but cannot be dealt with further here (158).

6. AUTOTROPISM (159)

It is necessary to consider here a phenomenon of general occurrence in which not external factors but changes within the plant itself serve as a stimulus. Thus it may be generally observed that every tropistic curvature, whether brought about by gravity, light, or other external factors, is followed, some time after the stimulus has ceased to act, by a straightening. This is mostly effected by elongations due to growth, but in curved roots may depend on contraction (p. 279). A similar behaviour is even seen after curvatures due to a forcible mechanical bending of an organ. This attempt of an originally straight organ to again become straight or of a curved organ to resume its original form is known as AUTOTROPISM.

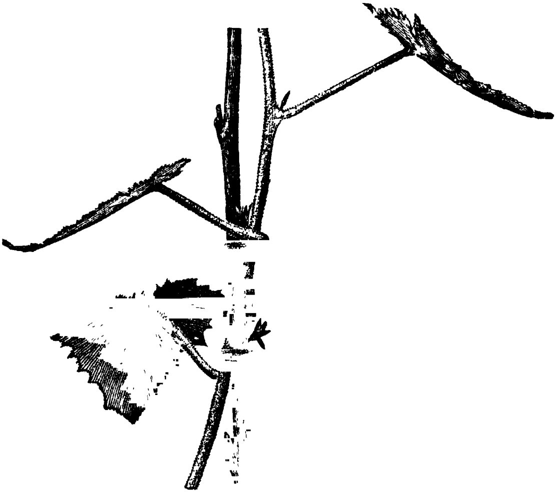


FIG. 289.—Part of a climbing shoot of *Maurandia scandens*. The lower portions of the leaf-stalks encircle the slender support in a tendril-like fashion. (After NOLL.)

Some such autotropic phenomena have been already referred to. Thus it was noted in relation to geotropism that curvature beyond the vertical was autotropically corrected. It has now to be added that every geotropic curvature retrogrades more or less when the one-sided stimulation is removed by rotating the object on the klinostat. In the same way phototropic curvatures lessen when the unequal illumination is stopped. Tendrils which have curved haptotropically straighten out when the contact-stimulus is removed. Even when the one-sided stimulation continues, there is often a certain degree of return observable in tropistic curvatures.

It is evident that the physiological effectiveness of the stimulus diminishes with its continued action. The correction of a curvature may effect complete straightening and may even sometimes go beyond this, and lead to a new curvature in the opposite direction. This will be in its turn autotropically corrected and thus a to and fro bending of a shoot may result from a tropistic stimulation. The only pre-requisite for autotropic correction is that the plant should be still capable of growth. Nothing is known as to the effective stimulus which leads to the restoration of the original form; it may be suggested that the plant reacts to internal tensions. Thus it is further found that the tensions arising by mechanical hindrance of a tropistic curvature are corrected in time by autotropism.

(b) Nastic Movements (160)

In the tropistic and tactic movements of irritability, the direction of the stimulus stands in direct relation to the direction of the movement; the nastic movements, on the other hand, are either brought about by diffuse stimuli with no definite direction or are not influenced by the direction of the stimulus. Such movements are thus confined to dorsiventral organs. The direction of the movement always depends on the reacting organ and not on the environment; the movements are not movements of orientation such as those we have hitherto considered. Their ecological significance is frequently obscure and according to GOEBEL they are in part useless movements.

Typical nastic movements of variation are shown by stomata (161); the structural relations of these determines the opening or closing of the pore by changes in the curvature of the guard-cells brought about by variations in their turgescence. It is frequently assumed that the closing on loss of water and the opening on illumination are purely mechanical results. Loss of water will have as its direct result a diminution of the osmotic pressure, and illumination will increase the pressure by increasing the production of assimilates. It cannot, however, be doubted that in addition to purely physical influences stimuli play a part. Thus light and some other factors also may act as stimuli directing the production of osmotic substances by the protoplasm.

In other nastic movements, as in the case of the stomata, light and heat, chemical substances, and sometimes also vibrations, may play the part of stimuli. Often the movement of a particular organ results from several of these stimuli acting in the same or in similar ways.

1. NYCTINASTIC MOVEMENTS (162)

Many foliage leaves and floral leaves assume different positions by day and by night. According as the change from the one position to the other is brought about by variations in the intensity of light, in the temperature, or in both factors at once, we distinguish between photonasty, thermonasty, and nyctinasty. The movements are carried out partly as growth-movements, partly as variation-movements.

a. THERMONASTY.—Growth-movements due to variations in temperature are found especially in flowers, *e.g.* *Crocus*, Tulip, *Ornithogalum*, *Colchicum*, and *Adonis*. These flowers on a rise of temperature exhibit a sudden and limited acceleration of the growth of their perianth-leaves or petals mainly on the inner side. The flowers consequently open. On the other hand, they close on a fall in the temperature.

The flowers of the Tulip and Crocus are especially sensitive to changes of temperature. Closed flowers brought from the cold into a warm room open in a short time; with a difference of temperature of from 15°-20° they open in two to four minutes. Sensitive flowers of the Crocus react to a difference of ½° C., those of the Tulip to 2°-3° C.

b. PHOTONASTY.—In a similar fashion other flowers (*Nymphaea*, Cacti) and also the flower heads of Compositae (Fig. 290) open on illumination and close on darkening. The night-flowering plants, such as *Silene noctiflora*, *Victoria regia*, and species of *Nicotiana*, behave in an opposite manner.

The significance of these movements must lie in only exposing the sexual organs when insect-visits may be expected; at other times they are protected against injury by rough weather, especially by rain. The night-flowering plants are adapted to pollination by moths.

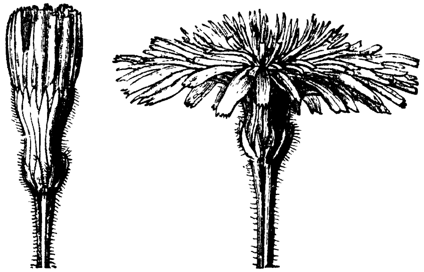


FIG. 290.—Flower-head of *Leontodon hastilis*, closed when kept in darkness, open when illuminated. (From DETMER's *Physiol. Pract.*)

c. NYCTINASTY.—Many foliage leaves exhibit nyctinastic movements which are usually influenced more by light than by temperature. In some cases (*e.g.* in Chenopodiaceae, Caryophyllaceae, Balsamineae, and some Compositae) these movements are entirely growth-movements, as in the floral leaves; in the Leguminosae, Oxalideae, and other plants provided with pulvini, variation-movements are found. The former are naturally of short duration and cease when the leaves are full-grown. The latter, however, continue for a long period. In the movements of variation an increase of turgor probably takes place in darkness in both halves of the pulvinus, but more weakly or slowly on the concave side. The night-position (sometimes called sleep-position though these movements have nothing to do with the sleep of animals) is always characterised by a vertical position of the laminae, the leaf-stalk or the pulvinus curving either upwards or downwards; the laminae themselves have thus either their under or upper faces turned outwards. In the day-position the surfaces stand horizontally or at right angles to the incident light (Fig. 291).

That these phenomena are not due to phototropism is shown by the day-position being assumed whether the under or the upper side is more strongly lighted or when the illumination is equal. The same holds for the effect of darkness.

Excessively high temperature or illumination causes the leaves to depart from the usual *day-position and to assume a different one; this is either externally similar to the night-position or is diametrically opposite to this. Thus the leaflets of Robinia are bent downwards at night, in diffused daylight they are spread out flat,* while in the hot mid-day sunlight they stand vertical. This so-called diurnal sleep is only found in leaves with pulvini and is brought about in a different way to the evening change of position; there is no increase of turgescence but a condition of flaccidity, which is unequal on the two sides of the pulvinus. (163)

PERIODIC MOVEMENTS (164)

When leaves have carried out regular nyctinastic movements for a long period under the influence of the alternation of day and night, the periodic movements continue for some days in constant light or constant darkness. In some plants it is possible to bring about experimentally a shorter or longer period of change than the usual one of twenty-four hours; this new periodicity also shows an after effect.

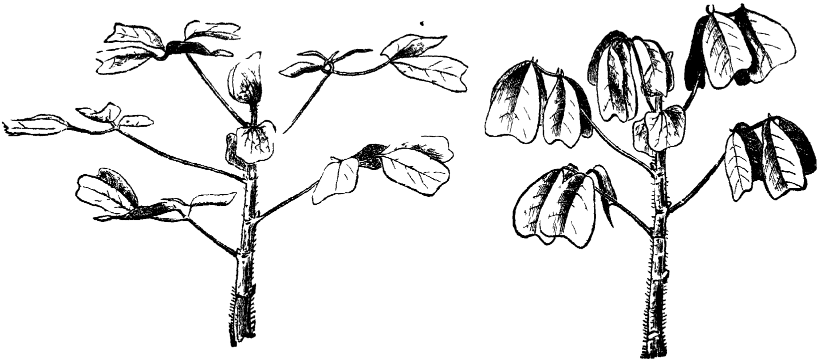


FIG. 291.—*Amicia zygomeris*, showing diurnal and nocturnal position of leaves.

On the other hand, it is established that, in certain flowers (*Calendula*) and leaves (*Phaseolus*), there are also movements with a period of 24 hours, determined not by the rhythm of light and darkness or their after effect. The possibility that these movements are autonomous is excluded. It can only be anticipated that some unrecognised factor will be found which determines this periodicity. The view of STOPPEL that variations of electrical conductivity in the atmosphere were of importance has not been confirmed.

2. CHEMONASTY (165)

Chemonasty bears the same relation to chemotropism as photonasty does to phototropism. From whatever side a chemical stimulus (such as the vapour of ether, chloroform, or ammonia) acts on a sensitive tendril the same side of the latter always becomes concave; this is the side which is especially sensitive to haptotropic stimulation.

These chemonastic curvatures of tendrils are evidently of no use to the plants. The same is the case for the nastic movements of tendrils which take place on wounding and on rise of temperature (traumatonasty, thermonasty).

On the other hand, chemonastic movements play an important part in some insectivorous plants. Very striking chemonastic movements are exhibited by the tentacles of Drosera (Fig. 207). On chemical stimulation these curve so that their upper sides become concave and the glandular heads are thus brought towards the centre of the circular leaf. Such substances as albumin, phosphates, etc., which *Drosera* can use as food, serve as stimuli (p. 176); so also can indifferent and even poisonous substances. Often minimal traces of these substances (*e.g.* 0·0004 mgr. of ammonium phosphate) suffice to bring about the irritable movement; when the stimulus is applied to the summit of the tentacle it leads to curvature at the base of the latter. There is thus in this case as in certain phototropic curvatures, but even more clearly than in these, a separation between the organ of perception which receives the stimulus and the motile organ that effects the movement. The stimulus received by the head of the tentacle must be conducted to the base of the latter.

An insect that has settled on a marginal tentacle will be brought by this curvature to the centre of the lamina. The short-stalked tentacles borne here send a stimulus to all the marginal ones, causing them to curve inwards. The insect is thus surrounded by many glands and covered with their digestive secretion.

The curvature resulting from growth is carried out in the same way as in tendrils. After curvature the tentacle has become considerably longer. When growth ceases, the motility of the tentacles is ended so that they can only close over a limited number of times. Further, the tentacles of *Drosera* in common with tendrils can exhibit haptonastic, traumatonastic, and thermonastic reactions. Doubtless, however, their chemonastic irritability is the main and most important one. Chemical stimuli are concerned in the movements of other insectivorous plants, *e.g. Dionaea* and *Pinguicula.*

3. SEISMONASTY AND TRAUMATONASTY (166)

In *Dionaea* the two halves of the leaf-blade (Fig. 210) close together not only as a result of chemical stimuli but also owing to a mechanical stimulus. In contrast to the haptotropic movements of tendrils or of *Drosera* resulting from contact with solid bodies, in the case under consideration every disturbance resulting from a mechanical shock acts as a stimulus; the movement can thus be brought about by rain-drops. These movements are termed seismonastic.

The most familiar example of seismonastic movements is furnished by *Mimosa pudica,* a tropical leguminous shrubby plant, which owes its name of Sensitive Plant to its extreme sensitiveness to contact. The leaves of this plant are doubly compound (Figs. 292, 293). The four secondary leaf-stalks, to which closely crowded leaflets are attached left and right, are articulated by well-developed pulvini with the primary leaf-stalks; while they, in turn, as well as the leaflets, are similarly provided with motile organs. Thus all these different parts are capable of movement, and the appearance of the entire leaf can become, in consequence, greatly modified. In their unirritated, light position (Fig. 292) the leaf-stalk is directed obliquely upwards, while the secondary petioles with their leaflets are extended almost in one plane. Upon any vibration of the leaf, in favourable conditions of temperature (25°-30° C.) and moisture, all its parts perform rapid movements. The leaflets fold together, and, at the same time, move forward; the secondary petioles lay themselves laterally together; while the primary leaf-stalk sinks downwards (Fig. 293). Leaves thus affected, if left undisturbed, soon resume their former position.

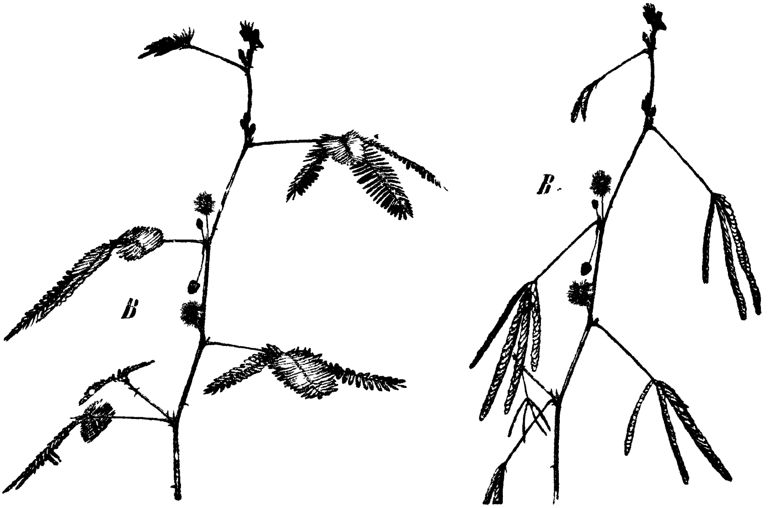


Fig. 292. Fig. 293.

Figs. 292, 293.—*Mimosa pudica*, with leaves in normal, diurnal position (Fig. 292), to the right, in the position assumed on stimulation (Fig. 293); *B*, inflorescences.

The position of a disturbed leaf is externally similar to its sleep- or night-position, but the conditions of tension in the pulvinus which lead to the two positions differ; in the night-position the leaf is still irritable to mechanical disturbance. The seismonastic, like the sleep-position, is caused by variations in turgor, but depends on a diminution of the osmotic pressure and a flaccid condition of the half of the pulvinus that becomes concave. This condition can be most clearly recognised in the irritable under side of the main pulvinus of the leaf; it is connected with an escape of liquid from the cells into the adjoining intercellular spaces.

The same position as is assumed by the leaf of *Mimosa* when touched results also from wounding (cutting, burning, corrosion).

The changes in the pulvini are the same on such traumatonastic stimulation as on the seismonastic. Similarly on applying other stimuli (electric shocks, sudden changes of temperature, or chemical stimuli) the same movements of the leaves are observed as on the stimulus of contact.

These stimuli are not restricted to the pulvinus first affected but are conducted for a considerable distance, in extreme cases through the whole plant, and at every pulvinus lead to a movement. The quickest and most extensive conduction of the stimulus is found when a traumatic stimulus is applied (^{167}), for instance, by holding a burning match near the leaflets of one of the pinnae. The leaflets directly affected by the flame fold quickly upwards, and this movement is performed successively by each pair of leaflets of the pinna until the articulation with the primary leaf-stalk is reached. The stimulation is then conveyed to the other pinnae, the leaflets of which go through the same movement in the reverse order; finally, the secondary petioles themselves draw together. Suddenly, when the whole process seems apparently finished, the main leaf-stalk in turn makes a downward movement. From this leaf the stimulus is able to travel still farther through the stem, and it may thus induce movement in leaves 50 cm. distant. The stimulus can also be conducted from the roots to the leaves.

The rate of conduction of the stimulus may attain after wounding 10 cm. and after contact 3 cm. per second, and thus be of considerable rapidity. It is, however, greatly below the rate of conduction of the stimulus along human nerves. While it is not yet known with certainty how the stimulus is conducted in *Mimosa*, it is clear that the process differs both from the conduction along nerves and from that in some other plants. The stimulus can certainly be carried across killed regions; it probably passes along the vessels of the wood and depends on the movement of water. According to RICCA it is possible to conduct the stimulus through a glass tube filled with water. This investigator supposes that there is a conduction of substances which arise on contact or wounding. The conduction of the stimulus seems to proceed somewhat differently according to whether it follows contact or wounding.

Some other Leguminosae and certain Oxalideae are similar but less irritable. Thus *Neptunia oleracea* and *Oxalis acetosella* exhibit movements on strong mechanical stimuli. These are much less considerable than in *Mimosa*. As a rule several shocks are required in these plants to start the reaction, while in *Mimosa* one is sufficient. The result of stimulation also increases with its increase while in *Mimosa* every effective stimulus under normal conditions starts the maximal movement. Movements of the leaves in response to wounding are also not confined to *Mimosa*.

The power of reaction to stimuli in *Mimosa* evidently depends on external factors, and each of these when in excess or lacking may lead to a state of rigor. Whenever the temperature of the surrounding air falls below a certain level (15°), no movements take place, and the whole plant passes into a condition known as COLD RIGOR, while, on the other hand, at a temperature of about 40°, HEAT RIGOR occurs. A DARK RIGOR is induced by a prolonged retention in darkness. In a vacuum, or on exposure to hydrogen and other gases—chloroform vapour, coal gas, etc.—movement also ceases, partly on account of insufficient oxygen, and partly from the actual poisonous action of the gases themselves. If the state of rigor is not continued too long, the original irritability will again return on the restoration of normal conditions. Similar conditions of rigor are met with in other cases of irritability.

The variation movements exhibited by the staminal leaves of some Berberidaceae (*Berberis*, *Mahonia*) and Compositae, especially beautifully by *Centaurea americana*, bear a certain relation to those of foliage leaves. The bow shaped filaments of the stamens of the Compositae straighten upon mechanical irritation. As they frequently contract 10-20 per cent of their length, the style becomes extended beyond the anther tube (Fig. 294). The reduction in the length of the filaments is accompanied by a moderate increase in their thickness due to the elastic contraction of the cell walls, and the consequent expulsion of water into the intercellular spaces. The stamens of *Berberis* and *Mahonia* are only sensitive to contact on the inner side near the base, and as their contraction occurs only on the inner side, the anthers are thus brought into contact with the stigma.

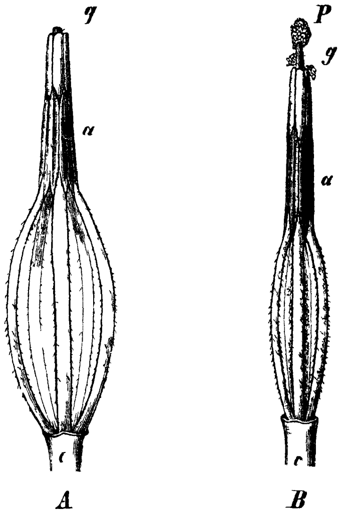


FIG. 294.—A single flower of *Centaurea jacea* with perianth removed. *A* Stamens in normal position; *B* stamens contracted; *c* lower part of tubular perianth; stamens; *a* anther tube; *g* style; *p*, pollen. (After PFEFFER; enlarged.)

The two lips of the stigmas of *Mimulus*, *Goldfussia*, *Martynia*, *Torenia*, and other plants close together when touched. In a short time they open and are again seismonastically sensitive. Opening also takes place when pollen has been brought to the stigma and germinated on it. The destructive effect of the pollen on the stigmatic tissues then leads, however, to a closing movement which is not a phenomenon of irritability.

While the extremes of haptotropism on the one hand and seismonasty on the other are very distinct forms of irritability, there are plants which exhibit a perception intermediate between irritability to contact and to shock. This applies to certain etiolated seedlings, the haptotropism of which was mentioned above; a jet of water or gelatine is sufficient to stimulate them, though more weakly than stroking with solid bodies (168).

As regards the mechanism of the movement all seismonastic plants follow the type of *Mimosa*. In *Dionaea* on the other hand the movement is effected by growth, as in tendrils.

PART II

SPECIAL BOTANY

DIVISION I

THALLOPHYTA. BRYOPHYTA. PTERIDOPHYTA

SPECIAL BOTANY

SPECIAL Botany is concerned with the special morphology, physiology, and ecology of plants. While it is the province of general botany to ascertain the laws that hold for the structure, vital processes, and the adaptations in the whole vegetable kingdom, it is the task of special botany to deal with the separate groups of plants. It is the endeavour of special morphology to obtain some insight into the PHYLOGENY OF THE VEGETABLE KINGDOM by morphological comparison of the manifold types of plants. The solution of this problem would provide the key for the construction of a NATURAL SYSTEM of classification of plants based upon their actual relationships. Such a system must necessarily be very imperfect, as it is not possible to determine directly the phylogenetic connection of different plants, but only to infer their relationships indirectly from morphological comparisons.

Such a natural system, founded on the actual relationship existing between different plants, stands in direct opposition to the ARTIFICIAL SYSTEM, to which has never been attributed more than a practical value in grouping the plants in such a manner that they could easily be determined and classified. Of all the earlier artificial systems, the sexual system proposed by LINNAEUS in the year 1735 is the only one which need be considered.

LINNAEUS, in establishing his classification, utilised characteristics which referred exclusively to the sexual organs, and on this basis distinguished twenty-four classes of plants. In the last or twenty-fourth class he included all such plants as were devoid of any visible sexual organs, and termed them collectively CRYPTOGAMS. Of the Cryptogams there were at that time but comparatively few forms known, and the complicated methods of reproduction of this large group of plants were absolutely unknown. In contrast to the Cryptogams, the other twenty-three classes were distinguished as PHANEROGAMS or plants whose flowers with their sexual organs could be easily seen. LINNAEUS divided the Phanerogams, according to the distribution of the sexes in their flowers, into such as possessed hermaphrodite flowers (Classes I.-XX.), and those in which the flowers were unisexual (XXI.-XXIII.). Plants with hermaphrodite flowers he again divided into three groups: those with free stamens (I.-XV.), which he further distinguished according to the number, mode of insertion, and relative length of the stamens; those with stamens united with each other (XVI.-XIX.); and those in which the stamens were united with the pistil (XX.). Each of the twenty-four classes was similarly subdivided into orders. While some of the classes and orders thus constituted represent naturally related groups, although by the method of their arrangement in the artificial system they are isolated and widely removed from their proper position, they include, for the most part, plants which phylogenetically are very far apart.

LINNAEUS himself (1738) felt the necessity of establishing natural families in which the plants should be arranged according to their "relationships." So long, however, as the belief in the immutability of species prevailed, the expressions relationship and family could have no more than a hypothetical meaning, and merely indicated a supposed agreement between plants having similar external forms. A true basis for a natural system of classification of organisms was first afforded by the theory of evolution.

The system adopted as the basis of the following description and systematic arrangement of plants is the natural system of ALEXANDER BRAUN, as modified and further perfected by EICHLER, ENGLER, WETTSTEIN, and others.

The vegetable kingdom may be divided into the following four main groups:

1. Thallophyta.
2. Bryophyta.
3. Pteridophyta.
4. Spermatophyta.

DIVISION I

THALLOPHYTA. BRYOPHYTA. PTERIDOPHYTA

Since the time of LINNAEUS the Thallophytes, Bryophytes, and Pteridophytes have been termed collectively Cryptogams in contrast to the Phanerogams or Spermatophyta. These two main divisions are, however, of unequal systematic value, for the lower Phanerogams approach the Pteridophyta, from which they have originated, more closely than these most highly developed Cryptogams approach the Bryophyta. The Bryophyta and the Thallophyta agree in being composed of more or less uniform cells, and are contrasted as CELLULAR PLANTS with the VASCULAR PLANTS comprising the Pteridophyta and Spermatophyta. Since, however, the Bryophyta and Pteridophyta agree in many respects, and appear to have diverged from a common source, the distinction of cellular and vascular plants must not be too strongly insisted upon.

The Spermatophyta are distinguished by their distribution by means of SEEDS from the Cryptogams, which form SPORES. Spores are unicellular structures which become separated from the parent-plant, and form the starting-point of the development of a new individual. The Cryptogams might, therefore, be termed spore-plants. The seed-plants also produce spores, but the sporangium and contained spore, which as a special structure develops into the seed, continues its development while still connected with the parent-plant, the seeds being ultimately separated from this.

The Bryophyta and Pteridophyta are united as the Archegoniatae on account of the structural agreement in their female reproductive organs or archegonia. These organs are also present in a somewhat simplified form in the lower Spermatophyta (in most Gymnosperms), so that a sharp line cannot be drawn between the Archegoniatae and higher groups of plants.

I. THALLOPHYTA (1)

It was formerly customary to divide the Thallophyta into Algae, Fungi, and Lichens. The Algae are Thallophytes which possess chromatophores with pigments, particularly chlorophyll; they are, therefore, capable of assimilating and providing independently for their own nutrition (autotrophic). The Fungi, on the other hand, are colourless and have a saprophytic or parasitic mode of life (heterotrophic). Such a method of classification, however, although possessing a physiological value, has no phylogenetic significance, as it does not express the natural relationships between the various groups. In the Lichens (Lichenes), which were formerly regarded as simple organisms, the thallus affords an instance of a symbiosis of Algae and Fungi. From a strictly systematic standpoint, the Fungi and Algae composing the Lichens should be classified separately, each in their own class; but the Lichens, among themselves, exhibit such a similarity in structure and mode of life, that a better conception of their characteristic peculiarities is obtained by their treatment as a distinct class.

The table of contents at the beginning of the book will afford a general survey of the arrangement of the classes which are treated of in order below.

CLASS I

Bacteria (1, 3-9)

Bacteria are organisms of extraordinarily small size (the smallest have a diameter of less than $\frac{1}{1000}$ mm.). They do not possess chlorophyll. The majority are unicellular, either spherical or rod-shaped, or their bodies have the form of a longer or shorter portion of a spiral (Figs. 77, 295). In a few cases the cells are branched (Fig. 296); in some they are united to form filaments (Figs. 297, 299).

A true nucleus is wanting in bacterial cells. Small granules (chromatin granules) can be demonstrated in the protoplasm by staining.

These occur singly or several in the cell, and are perhaps functionally similar structures to a nucleus.

In the protoplasm are minute vacuoles or spheres of reserve materials, consisting of carbohydrates (glycogen, but no starch and sugar) fats, and albuminous substances (volutin). The cell is enclosed by a thin membrane which is composed neither of cellulose nor of chitin. In some species the outer layers of the membrane swell greatly, so that the cells or cell-rows become embedded in mucilage; this condition is termed the zoogloea-stage (Fig. 298). A less marked development of mucilage produces the tubular sheaths of the filamentous bacteria (Fig. 299); in some species these sheaths harden and lose their connection with the cells, so that the filament is freely moveable within its sheath. When the filament grows actively it may rupture and the sheath be broken through laterally. The further growth of the lower portion of the filament, through the opening in the sheath, leads to the appearance of "false branching" (cf. p. 74). The mucilage in other cases may be secreted on one side of the cell and become a firm stalk in which compounds of iron may be deposited (*Gallionella ferruginea*, Fig. 300) (9b).

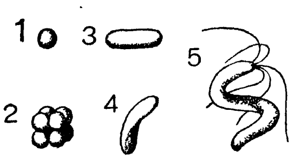


FIG. 295.—Shapes of Bacteria. 1, 2, Cocci (2, *Sarcina*); 3, Rod-shaped (*Bacillus*); 4, *Vibrio*; 5, *Spirillum*.

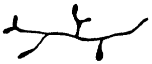


FIG. 296.—*Mycobacterium tuberculosis*. Branched cell. (After FUHRMANN.)

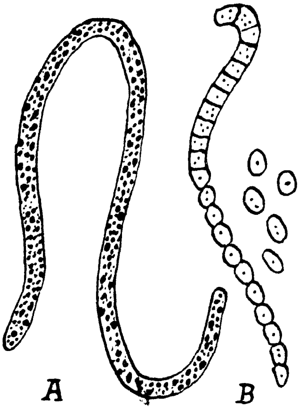


FIG. 297.—*Beggiatoa alba*. A, Filament with included droplets of sulphur, the transverse walls not evident; B, Filament with deficiency of sulphuretted hydrogen, separating into its individual cells. (× 600. After DÜGGELI.)

In certain stages of their development many Bacteria possess delicate protoplasmic cilia (3a) which pass through pores in the membrane and lead to the active movement of the cells (cf. p. 328).

The cilia are borne in various ways (Fig. 301). They may be distributed over the whole surface (peritrichous), single (monotrichous), or in a group springing from one point (lophotrichous). Certain filamentous bacteria have the power of creeping on a solid substratum (3b).

Bacteria increase in numbers by means of cell-division, which in the rod-shaped forms is always at right angles to the long axis. From this feature the Bacteria are sometimes called Fission-Fungi or Schizomycetes.

In some cases *e.g. Chromatium* (Fig. 302) two cells have been observed connected by a narrow bridge. It is not impossible that this "conjunction" (^{8c}) may represent a sexual process.

Under unfavourable conditions many bacteria form resting spores. The protoplasm contracts in the middle or near one end of the cell and surrounds itself with a new membrane, becoming an endospore, (Fig. 303 *c*). When the spore is mature the original wall of the parent-cell swells and disappears.

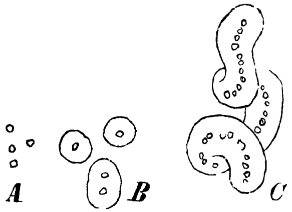


FIG. 298.—*Streptococcus mesenterioides*. *A*, Isolated cells without gelatinous sheath; *B*, *C*, formation of chain of cells with gelatinous sheath (× 620. After VAN TIEGHEM.)

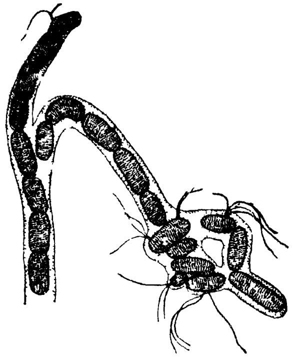


FIG. 299.—*Cladothrix dichotoma*. Formation of swarm-cells from the cells of the filament. (× 1000. After A. FISCHER.)

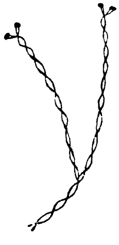


FIG. 300.—*Gallionella ferruginea*. Cells at the ends of the sheaths, which are twisted spirally round one another. (× 750. After CHOLODNY.)

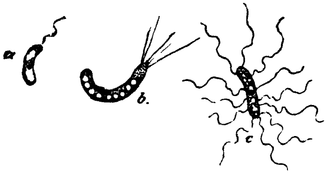


FIG. 301.—Types of arrangement of flagella. *a*, *Vibrio cholerae* (monotrichous); *b*, *Spirillum undula* (lophotrichous); *c*, *Bacillus typhi* (peritrichous). (× 2250. After A. FISCHER.)

Bacillus subtilis, the Hay Bacillus (Fig. 303), which appears as a rule in the decoction obtained by boiling hay in water, will afford an example of the life-history of a bacterium. The spores of this species, which withstand the effect of the boiling water, produce on germination rod-shaped swarming cells with cilia on all sides; these divide and may remain connected in short chains. At the surface of the fluid these swarming cells change into non-motile cells without cilia; these divide up, giving rise to long intertwined chains of cells. These are associated together in the pellicle covering the surface (zoogloea stage). Spore-formation occurs when the nutritive substances in the fluid are exhausted.

Occurrence and Mode of Life.—There are numerous species of bacteria, over a thousand, known. They are distributed over the whole earth, occurring in enormous numbers of individuals in water, in the soil, and in the dead and living bodies of animals and plants. They are widely distributed with the dust in the atmosphere. 1 grm. of garden soil contains some 50–100 million bacteria, and 1 mg. of fresh human faeces 20–165 million. The wide distribution of bacteria is mainly due to three factors: their rapidity of multiplication, the resistance of their vegetative cells and spores to unfavourable conditions, and the variety in their methods of nutrition.

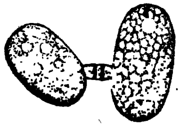


FIG. 302.—*Chromatium okenii.* Conjunction of two cells. (× 1500. After POTTHOFF.)

Under optimal conditions some bacteria can divide several times in an hour, so that a single individual could give rise in 24 hours to several million descendants.

The spores of bacteria are extremely resistant to desiccation, chemically active substances (disinfectants), and extremes of temperature. Some can endure for a short period both the temperature of liquid hydrogen (about −253° C.) and that of boiling water. Even the vegetative cells of many species are very resistant to drying, but are usually killed by a few minutes in water at 60° C. Some can live at higher temperatures than this, for example, in the water of hot springs. Others show an active production of heat by their respiration (spontaneous heating of damp hay, dung, tobacco, cotton-wool by *Bacillus calfactor*).

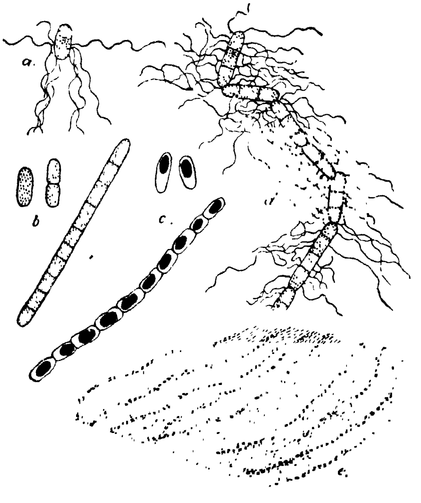


FIG. 303.—*Bacillus subtilis.* *a*, *d*, Motile cells and chain of cells; *b*, non-motile cells and chains of cells; *c*, spores from the zoogloea, *e*. (*a-d* × 1500; *e* × 250. From A. FISCHER, *Vorles. über Bacterien.*)

The nutrition of most bacteria is heterotrophic, either saprophytic or parasitic. Obligate parasitism is rare; the majority of pathogenic species can be grown apart from the animal or human body. Culture in suitable nutrient solutions (*e.g.* meat-juice with peptone) presents as a rule little difficulty. On solid substrata (gelatine, agar) the bacteria form mucilaginous colonies of various shapes (Fig 304); these are usually colourless, but in other cases of various tints (pigment bacteria). Bacteria, by means of enzymes cause profound changes in their nutrient substratum (putrefaction, decay), while pathogenic forms exert poisonous effects by means of toxins. Besides giving rise to diseases in man (Fig. 305) and animals, bacteria cause diseases of plants (*e.g.* a disease of the potato caused by *Bacillus phytophtorus*), cancer-like growths (crown-gall) on various plants by *Bacillus tumefaciens.*

Among peculiarities in the nutritive physiology of certain Bacteria (cf. p. 259) the following may be mentioned. Carbon-assimilation, in spite of the absence of chlorophyll and light, by means of energy produced by the oxidation of inorganic compounds; fixation of free nitrogen; nitrification; denitrification; anaerobic life. The photogenic bacteria produce a substance within their cells that is phosphorescent on oxidation (^{5}).

Bacteria sometimes suffer from a disease in which their cells completely break down. The cause of this, which is termed d'Hérelles' phenomenon, after its discoverer, is not completely understood. It is caused by what is known as a "bacteriophage," which, on the one hand, may be regarded as an extremely minute organism parasitic in the body of the bacterium, or on the other hand be regarded as an enzyme.

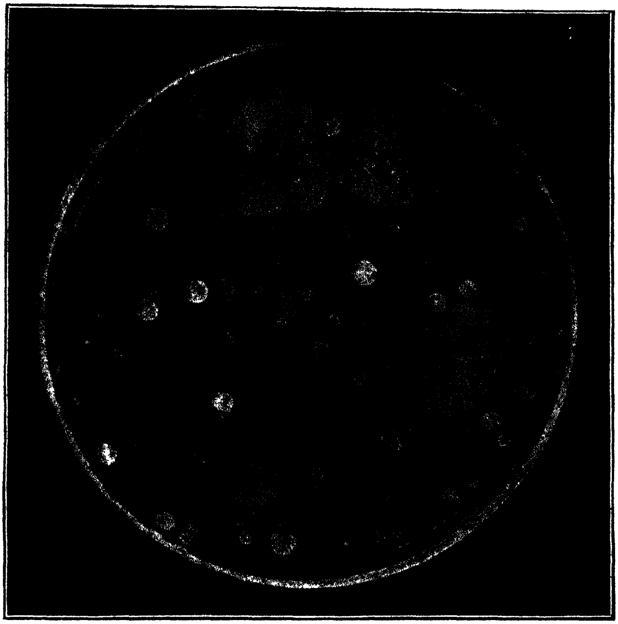


FIG. 304 —Plate of meat-agar exposed for one hour in an inhabited room, showing the colonies of bacteria which have developed after 6 days. ($\frac{4}{5}$ nat. size, after LIESKEI, *Kurzes Lehrb. d. allg. Bakterienkunde*, Borntrager, Berlin, 1926.)

Classification.—The division of the Bacteria into Orders is extremely difficult, since their mutual relations are incompletely known. The following subdivision is therefore of value as a survey of the group, rather than as an ultimate solution of the systematic problem.

Order 1, Eu-Bacteria.—Unicellular, unbranched Bacteria. This order includes the great majority of forms.

Family 1, Coccaceae.—Spherical bacteria. Genera: *Streptococcus*, spherical cells united in rows: *Micrococcus*, cell-divisions in two directions of space: *Sarcina* (Fig. 295), cell-divisions in three directions of space, the colonies therefore forming cubical packets. A number of species of *Streptococcus* give rise to suppuration, *e.g. Micrococcus pyogenes aureus*: *M. gonorrhoeae* (Fig. 305) causes gonorrhoea: *Sarcina lutea*, which is not pathogenic and forms yellow colonies, is common in human surroundings.

Family 2, Bacteriaceae.—Rod-shaped bacteria which do not form spores. Genus, *Bacterium*. *Bacterium nitosomonas*, forms nitrites from ammonia; *B. nitrobacter*, forms nitrates from nitrites; both are autotrophic and occur in all soils: *B. radicicola*, fixes nitrogen in the root-nodules of Leguminosae: *B. aceti*, oxidises alcohol to acetic acid: *B. acidi lactici*, causes milk to turn sour: *B. phosphorescens*, causes phosphorescence of fish and meat: *B. prodigiosum*, forms red colonies on bread, etc. ("the bleeding host"); *B. vulgare* (=*Proteus vulgaris*) causes ill-smelling putrefactions: *B. coli*, the commonest intestinal bacterium: *B. dysenterieae*, *typhi*, *pestis*, *influenzae*, give rise respectively to dysentery, typhoid fever, plague and influenza.

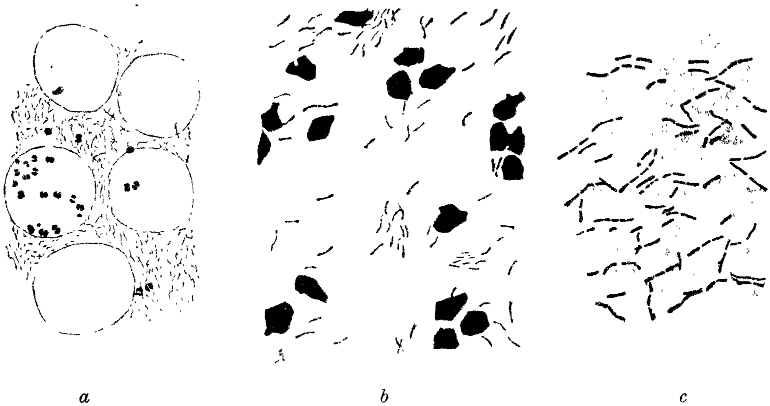


FIG. 305.—Stained preparations from Ziegler's *Text-book of Pathology*. *a*, Gonococci in the gonorrhoeal discharge, mucus and pus corpuscles with cocci (methylene blue and eosin), × 700; *b*, tubercle bacilli in sputum of phthisis (fuchsin and methylene blue), × 400; *c*, splenic fever bacilli in the pustule of the disease (methylene blue and vesuvin), × 350. (From A. FISCHER, *Vorles. über Bacterien.*)

Family 3, Bacillaceae.—Rod-shaped bacteria, which form spores. Genus, *Bacillus*. *Bacillus subtilis*, Hay Bacillus (Fig. 303); *B. butyricus*, forms butyric acid; *B. amylobacter*, decomposes cellulose; *B. anthracis*, which causes splenic fever (Fig. 305 c), was the first bacterium to be shown to be the cause of a disease by ROBERT KOCH. Anaerobic; *Bacillus saccharobutyricus* (*Clostridium Pasteurianum*), fixes nitrogen in the soil; *B. tetani*, tetanus bacillus.

Family 4, Spirillaceae.—Spirally wound bacteria. Genera: *Vibrio* (Fig. 295, 4), comma bacillus, representing a portion of a spiral turn: *Spirillum* (Fig. 295, 5), spirally wound. Non-pathogenic forms of *Vibrio* and *Spirillum* occur in water; also *Vibrio cholerae*, the cause of cholera (Fig. 301 *a*).

Order 2, Mycobacteria (8, 75).—The rod-shaped, non-motile cells exhibit true branching (Fig. 296) under certain conditions of cultivation. This is infrequent in *Mycobacterium*, but is the rule in *Actinomycetes*.

Mycobacterium diphtheriae, causes diphtheria ; *M. tuberculosis*, the Tubercle Bacillus (Figs. 296, 305), usually grows as slender, non-motile rods, without spores, but may also give rise to branched forms.

The Actinomycetes (75), which are placed here with some reservations, grow in artificial cultures to an organism of several centimetres diameter, consisting of a single, highly branched, and extremely slender cell (diameter 0·5—1·0 μ). When filaments project into the air, their contents segment, and the portions later, on the breaking down of the parent filament, become free as spores. Under certain external conditions the Actinomycetes grow in the form of rods which are indistinguishable from true bacteria. *Actinomyces bovis* gives rise to Actinomycosis, forming swellings in the bodies of animals and human beings. *A. scabies* gives rise to a scab of Potatoes and Turnips. Other species are widely distributed as saprophytes.

Order 3, Trichobacteria, Filamentous Bacteria.—The cells are united to form unbranched, or falsely branched, filaments.

Family 1, Chlamydobacteriaceae.—The attached filaments are enclosed in a sheath, within which the cells may become isolated and emerge either in the non-motile condition or as ciliated cells (*Cladothrix dichotoma*, Fig. 299) ; these free cells later become attached and grow into new filaments. The best-known representatives of the Family are : *Cladothrix dichotoma*, the falsely branched filaments of which form a slimy growth on algae, stones and wood in water ; *Crenothrix polyspora* with swarm-spores, and *Leptothrix ochracea* without, are species which do not show false branching. These two forms occur in swamps and ditches and accumulate hydrated oxide of iron in their sheaths (iron-bacteria) (9b) ; when they develop abundantly they may lead to the blocking of water pipes, and in the dead condition form a source from which iron is obtained.

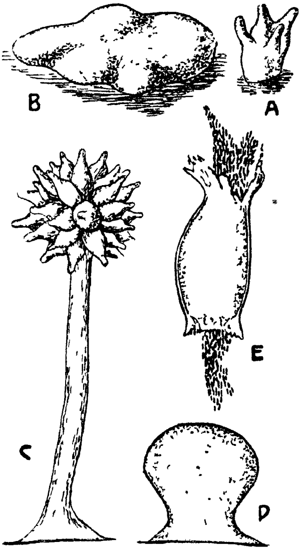


FIG. 306.—*A*, *Myxococcus digitatus*, bright red fructification occurring on dung (× 120) *B*, *Polyangium primigenium*, red fructification on dog's dung (× 40). *C*, *Chondromyces apiculatus*, orange fructification on antelope's dung. *D*, Young fructification (× 45). *E*, Single cyst germinating (× 200). (*A*, *B* after QUEHL ; *C-E* after THAXTER.)

Family 2, Beggiatoaceae.—The filaments have no sheath. They creep on the moist substratum, probably by minute contractions that proceed in a wave-like fashion along the filament. They reproduce by breaking of the filament into portions or into its constituent cells. These bacteria are autotrophic, and frequently form visible white layers on the bottom of sulphur springs containing sulphuretted hydrogen (sulphur bacteria) (4, 9a). *Beggiatoa alba*, widespread in fresh water (Fig. 297) ; *B. mirabilis*, which occurs in the East Sea at Schlick, is a giant among bacteria, forming filaments which are visible to the naked eye.

Order 4, Myxobacteria (16).—The colonies of Myxobacteria consist of a host of small rods, without cilia, which can move in a co-ordinated way by means of an excretion of mucilage, so that the "pseudoplasmodium" gives the impression of being a single individual (Fig. 306). The rods creep together and become heaped up at places to form minute and usually brightly-coloured fructifications; these may be stalked or not, the stalk and wall being derived by a transformation of mucilage. The fructifications correspond to cysts, within which the vegetative rods shorten and become spherical and so changed into spores. On germination these again grow into rods which swarm out of the ruptured cysts (Fig. 306). The Myxobacteria live saprophytically and mainly upon the dung of animals.

Order 5, Spirochaetales ($^{1, 9c}$).—The Spirochaetes are only placed here with reservations. Their slender body has no cilia, but shows a wavy curvature and an active snake-like movement. They are placed by various authors in relationship to the Protozoa, the Flagellates, or the Oscillarieae (Cyanophyceae), but ENGLER groups them with the Bacteria. *Spirochaete pallida* is the cause of syphilis and *S. recurrentis* of relapsing fever. Non-pathogenic forms are of frequent occurrence in the mouth.

Relationships ($^{1, 9d}$).—The position of the Bacteria in the genealogical tree of plants is still a matter of uncertainty. They might be derived forms from Algae and Fungi, which had lost their chlorophyll and diminished in size. An attractive view is to regard them as primitive organisms on account of their simple cellular structure with no nucleus and the capacity of some kinds to live autotrophically.

No sure connections by relationship can be demonstrated between the Bacteria and any other Class, not even to the Cyanophyceae, along with which they have been grouped as Schizophyta. Fossil Bacteria are known from the Palaeozoic rocks.

Survey of the Orders of Bacteria :

Eu-Bacteria—Unicellular, unbranched.
Mycobacteria—Cells sometimes with true branching.
Trichobacteria—Cells connected to form unbranched or falsely-branched filaments.
Myxobacteria—Unicellular individuals united in colonies.
Spirochaetales—Unicellular, body flexible.

CLASS II

Cyanophyceae, Blue-green Algae ($^{1, 10}$)

The Cyanophyceae are unicellular or filamentous Algae of primitive organisation; they are mostly blue-green in colour and their nutrition is autotrophic. The cell-walls consist of cellulose and pectic substance, and frequently show mucilaginous swelling; in the protoplasts a distinction can be made of an inner colourless region (centroplasm) and around this a peripheral region usually of a blue-green colour in the form of a hollow sphere (chromoplasm). There are neither definite chromatophores nor vacuoles, and the cell does not possess a true nucleus.

The pigments are diffusely distributed in the chrom defined from the central region. In addition to chloro two pigments soluble in water, phycocyan and phycoe some species. The relative proportions in which the pi extent liable to changes, so that the tint may sometimes times more inclined to blue. This is especially the ca exhibit what is known as CHROMATIC ADAPTATION. In mainly red pigment, and in red light mainly green and bl same species appears as red and green forms, complement light. Starch is never formed as a reserve product, its place being taken by a glycoprotein derived from glycogen.

Bodies of protein nature in the form of short filaments are present, singly or in groups in the colourless centroplasm. The latter may have some of the functions of a nucleus, but a true well-defined nucleus is wanting throughout the group; in cell-division no chromosomes are formed and the process is one of simple constriction.

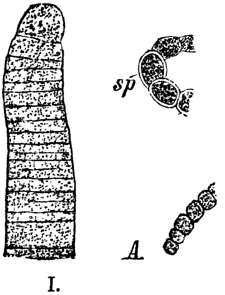


FIG. 307.—I. *Oscillaria prince* tion of a filament. (× 10 BURGER.) II. *Nostoc Linck* floats freely in water. *A* heterocysts (*h*) and *B*, isolated spor *C*, young fil (× 650. Aft

Sexual reproduction is unknown. Reproduction depends on the active cell-division, on which account the name Schizophyceae is sometimes applied to the group. The cell-rows of the filamentous species separate into short lengths called HORMOGONIA; these are capable of creeping movements and give rise to new plants. In SPORES are formed by the enlargement of cer their walls, and storage with reserve food-m a means of persisting through unfavourable pe

Most Cyanophyceae are non-motile. Some filame movements on moist substrata. Cilia are wanting and due to the excretion of mucilage which swells in w plant-body ([10a, 9c]).

The simplest Cyanophyceae (*e.g.*, *Chroococcus*) co cells. In *Gloeocapsa* (Fig. 34) the species of which f walls or rocks, the cells remain connected by their st form multicellular colonies.

In the filamentous Hormogoneae the cells are conn filaments are sometimes unbranched and in other ca (Fig. 82). In the Oscillarieae, which are common in w filament is composed of disc-shaped cells (Fig. 307, I).

s of cells, which form spherical or irregular mucilaginous
Nostoc, and in many other Cyanophyceae, single cells at
laments form HETEROCYSTS (Fig. 307, II *h*); these are
y pigments having disappeared, while the wall is some-
le these structures are functionless, but in a few cases
new filaments.

ae are distributed over the whole earth as
or sheets of fine filaments occurring in water
, on moist, muddy soils and on the bark of trees.
nportant part in the first colonisation of exposed

eae live as plankton in the surface waters of lakes and
with the so-called "water bloom"; in the warmer seas
acum forms a "sea bloom" which gives the water a red
ome Blue-green Algae occur along with Fungi as constituents
ve endophytically in cavities in the tissues of other plants;
s in *Azolla*, and by assimilating the free nitrogen of the air
ce for the latter plant as the nodule bacteria have for the
case of some other Cyanophyceae also the power of fixing
een demonstrated (10b).

ships of the Cyanophyceae to other groups of organisms
ncertain. On account of the great lack of differentia-
ell-contents they are probably to be regarded as per-
forms, which have not undergone further development.

condition the Cyanophyceae are known, though often with some
m the Cambrian onwards.
e Orders:
—Unicellular or colonial; without hormogonia or heterocysts.
Filamentous, with protoplasmic connections between the cells; hormogonia always and heterocysts frequently present.

CLASS III

e (Flagellates) (1, 11, 12, 17-19, 27)

small unicellular organisms with a true nucleus,
ers somewhat from the nuclei found in the
12d). The protoplast exhibits contractile or
nd is limited by a denser protoplasmic layer
cell-wall. One or more cilia (flagella) are
ns. The protoplast contains a nucleus, a
n many species well-formed green, or brownish-
blue or red, chromatophores. A red eye-spot
The product of assimilation is usually oil, but
ydrates also occur. Other forms are colourless

and are saprophytic or obtain their food like ani of some Flagellates, especially of the colourless f amoeboid c exhibits cha creeping mo cases slender podia may be withdrawn as These assist of solid parti diatoms, green 308, 314).

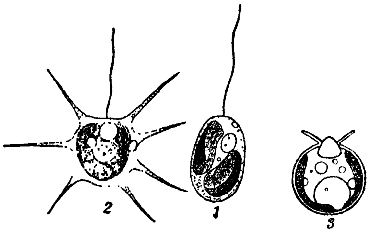


Fig. 308.—*Chrysamoeba radians.* Occurs in fresh water and has a single cilium and two brownish-yellow chromatophores. *1*, Ordinary form; *2*, amoeboid condition with radiating pseudopodia. (After Klebs); *3*, *Ochromonas.* Cyst with opening and plug. (After Pascher.)

Most repres group live as n others form mor cated cell-colonies by mucilage, or peculiar stalked or unstalked firm investments (Fig. 3 with siliceous (Silicoflagellatae) (Coccolithophorideae) skeletal st 310).

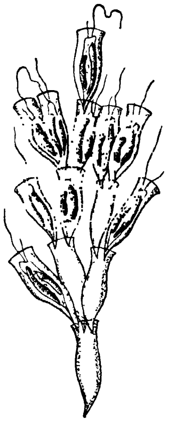


Fig. 309.—*Dinobryon Sertularia* (Cryptomonadales). Occurs in fresh-water plankton and forms invested colonies. (×450. After Senn.)

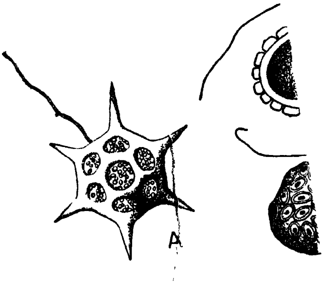


Fig. 310.—*A*, *Distephanus speculum.* (After *B*, *C*, *Calyptrosphaera insignis* from the *B* is in optical section and *C* in surfa (×1200. After Schiller.)

Multiplication takes place by division, and in many species resting spores or cysts are produced. On the germination of after division of the contents, a number of daughter-cells ma liberated. Sexual reproduction, by the conjugation of two cells only been observed in a few cases.

Flagellates live in all bodies of water, from puddles and gutters to the oc and often occur in enormous numbers, so that the water is coloured brown or gr ccolithophoridae have been estimated to occur in a cubic

es of colour met with in the Flagellatae, together e details of their structure enable the following ished.

-The radially symmetrical cells have one or two cilia and h the chlorophyll is more or less concealed by an imperfectly w pigment. On assimilation a special organic compound, med in addition to fat and oil. The endogenously formed all of which is usually silicified and has a pore closed by a especially characteristic of the

.—These also have a brown colour. ally compressed and thus dorsi- ntly have an obliquely truncated 311). Two cilia of unequal length anterior furrow or a gullet-like depression. Some forms have starch as the product of assimilation, around pyrenoids that occur free in the protoplast.

monas
After

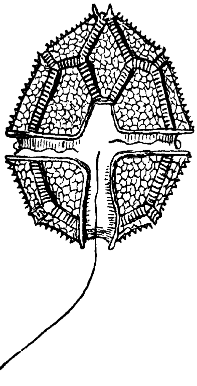


FIG. 312.—*Peridinium tubulatum.* (After SCHILLING.)

Dinoflagellatae (Peridineae) (1, 11, 17-19).—These are highly developed Flagellates. They occur as unicellular, free-swimming organisms in fresh water, but for the most part in the sea, where, together with the Coccolithophorideae and Diatomeae, they constitute an important con- the phyto-plankton. Their cells are characterised by the pos- two long ribbon-shaped cilia or flagella which spring from the the ventral surface in a longitudinal furrow; one of the cilia backwards, the other is thrown into curves and lies in a transverse g. 312). The protoplast has a nucleus, vacuoles of different sorts, rous brownish-yellow chromatophores; the latter contain a mixture of gments. Starch or oil is formed as the product of assimilation. While odiniaceae (Fig. 318 *d*) have naked cells, the typical Peridiniaceae have a ied of polygonal plates composed of cellulose; these are usually delicately d and perforated with pores. The transverse furrow is formed by one aped plate (Fig. 312).

any Peridineae of the plankton the plates bear special wing-like expansions 13) or the cells have long horn-like processes. These adaptations enable ganisms to remain floating in the water (18). The form of the cell is very le; for instance in *Ceratium hirundinella* individuals with two, three, and orn-like processes are produced, under the influence of diverse thermic, l and chemical stimuli (19).

crease in numbers is effected by division of the cells which usually takes place e motile condition; when the wall is thick and sculptured it is usually ured.

Certain marine Dinoflagellates are phosphorescent and
the phosphorescence of the sea (5). Examples are *Cera*
divergens, and *Noctiluca miliaris.* The last named attain
and is placed in this group on account of the resemblan
Gymnodinium.

Heterochloridales.—This group is characterised by the
the chromatophores, the chlorophyll being mixed with a
turns blue with acids. They have always two unequal cilia and
products a fatty oil and leucosin, never starch.

Euglenales.—The green scum or "water-bloom" frequen
ponds may consist of *Euglena* (Fig 314). The elongated c

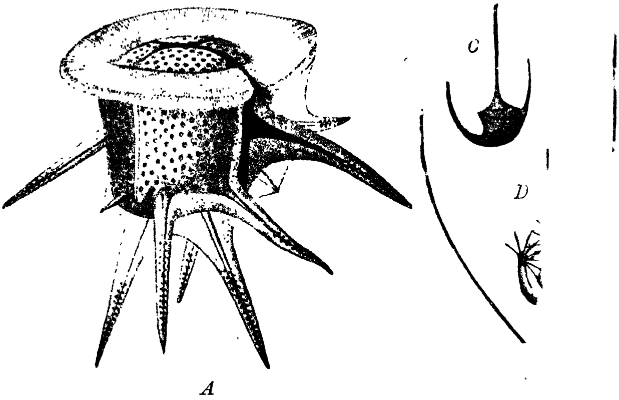


FIG. 313.—Peridineae of the plankton. *A*, *Ceratocorys horrida*
B, *Ceratium tripos intermedium* var. *aequatoriale*, Indian
gibberum, and *D*, *Ceratium palmatum*, Atlantic Ocean (×
Ocean (× 125). (After G. KARSTEN.)

flattened and are capable of metabolic changes of form.
flagellum, which arises at the anterior end from a gullet-
green chromatophores, a number of which are present in
substance called paramylon.

Polyblepharidales.—The naked cells are provided w
length. At the hinder end is a pure-green, cup-shaped
a pyrenoid around which starch is formed, While *Po*
by dividing in a longitudinal plane, more highly develo
Polytomella, *Phyllocardium*) have also sexual reproduct
divide to give rise to a number of ciliated gametes, wl
zygotes ; on the germination of the zygote four vegetati

In all the groups of Flagellates there ar
coloured autotrophic forms—also colourless form
ally ; these may even be able to ingest soli
pseudopodia (Fig. 315).

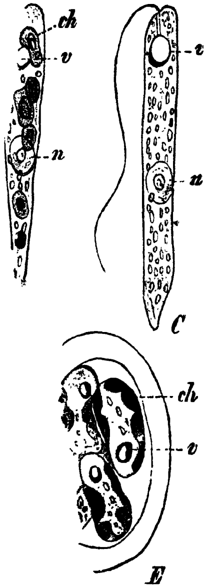
coloured species (*e.g. Euglena gracilis*) it has been found
lourless form with leucoplasts ; this is done by cultivating
rk in suitable organic food solutions *e.g.* 2–4% solution of
It has even been possible to obtain individuals without

tomonadinae, **Polymastiginae**) also are colourless and doubt-
netically from coloured ancestors. To the Protomonadinae belong certain forms that live in the blood and the gut of animals and give rise to some tropical diseases. Thus *Trypanosoma Brucei* causes the Tsetse-disease of cattle, and *T. gambiense* (Fig. 316) the sleeping sickness in man ; both are conveyed by flies belonging to the genus *Glossina.* Plants also may be infected by colourless Flagellates.

In spite of differences in colouring, the Chrysomonadales and the Hetorochloridales are closely related, and so also the Cryptomonadales and the Dinoflagellatae; the Euglenales and the Polyblepharidales are isolated groups.

Some Flagellates with sculptured walls have been preserved as fossils. Thus Silicoflagellates are known from the Cretaceous period, Dinoflagellates from the Jurassic, and Coccoliths even from the Cambrian.

Key to the Orders of Coloured Flagellates :—



rm with green
us ; *v*, vacuole and
, Hemi-saprophytic
'omatophores. *C*,
occurring in nutrient
D, Resting cyst of
E, Germination of
A by division into
er escape. (*A*, *C* ×
After ZUMSTEIN.)

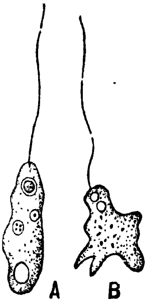


FIG. 315.—*Mastigamoeba invertens.* A colourless Flagellate. *A*, Free swimming. *B*, Amoeboid condition. (×1033. After LEMMERMANN.)

wn, radially symmetrical, 1 or 2 flagella, characteristic

wn, dorsiventral, 2 unequally long flagella.
n, dorsiventral, 2 unequally long, ribbon-shaped flagella,
inal and transverse furrows.
llow-green, 2 unequally long flagella.
flagellum.
een, 2–8 equally long flagella.

rom the Flagellatae.—The Flagellates, as has
ceding account, exhibit great variety. In none

of the particular groups, however, can primitive forms be recognised; even those that appear most primitive must be regarded as derived from extinct and simpler types. On the other hand, more highly organised series of forms appear to have developed from most of the groups. The lowest animals (Rhizopoda) can be connected with the colourless Flagellates, while series of plant-like forms, which have recently been especially studied by PASCHER, are related to the pigmented groups. These derived forms begin with permanently motile, unicellular organisms; at a higher stage the cells are for the most part non-motile (Capsales and Coccales) and only liberate motile cells in reproduction; the highest stage in the development is reached by filamentous, usually attached forms (Trichales) which also produce motile swarm-spores The higher forms can in part be regarded as true Algae, without, however, attempting to draw any sharp line between the Algae and the Flagellates.

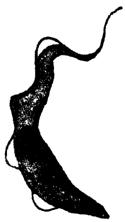


FIG. 316.—*Trypanosoma gambiense* From the blood of an infected monkey, the flagellum forming an undulating membrane. (After MINCHIN.)

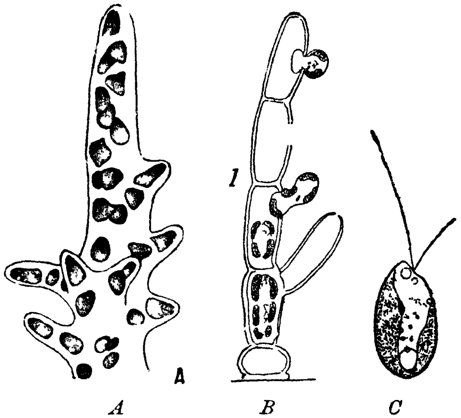


FIG. 317.—*Hydrurus foetidus.* *A*, Apex of a branch of the colony enclosed in mucilage. (After BERTHOLD.) *B*, *Phaeothamnion Borzianum.* Young plant forming zoospores, and showing the basal cell. (After BORZI.) *C*, Swarm-spore with chromatophore, eye-spot, sphere of leucosin at the hind end and two vacuoles at the anterior end, which bears two cilia. (After PASCHER.)

The **Chrysophyceae** are derived from the Chrysomonadales. *Hydrurus foetidus* has richly branched, firm, mucilaginous colonies (Fig 317, *A*) which may attain a length of 30 cm. *Phaeothamnion* has the highest organisation (Fig. 317); its branched filaments form small plants, under ¼ mm. long, which are attached to the surface of fresh-water species of *Cladophora* by means of a hemispherical basal cell. The swarm-spores which escape from the cells of the filament resemble the Chrysomonadinae, with a brown chromatophore, eye-spot, and two contractile vacuoles. When the swarm-spore becomes attached, it loses the cilia, contractile vacuoles, and eye-spot, and develops into a new filamentous plant. The silicified cysts, with pore and plug, of the Chrysomonadinae also occur among the Chrysophyceae.

The **Cryptophyceae** is another series derived from the Cryptomonadales.

The **Dinophyceae**, similarly related to the Dinoflagellatae, is a series commencing with unicellular non-motile forms like *Cystodinium* (Fig. 318), and attains its highest point in *Dinothrix* (Fig. 319) which forms irregular filaments consisting of a few cells. Both *Cystodinium* and *Dinothrix* liberate swarm-spores that resemble *Gymnodinium*

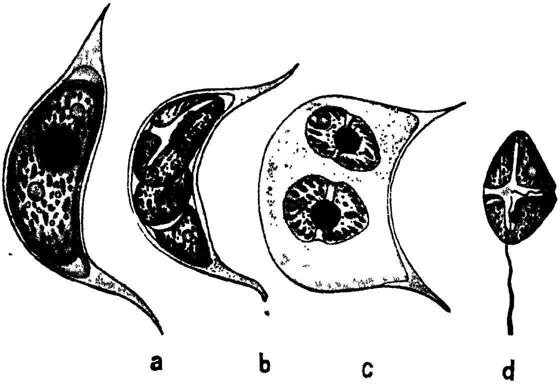


FIG. 318.—*Cystodinium Steinii*: *a*, cyst; *b*, division into two swarm-cells; *c*, a cyst swelling; *d*, liberated swarm-cell. (× 480. After KLEBS.)

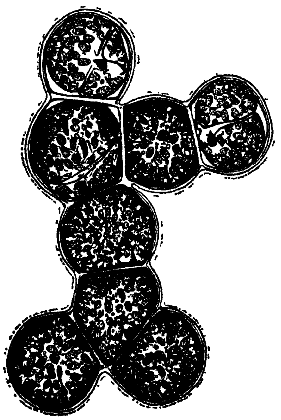


FIG. 319.—*Dinothrix* with *Gymnodinium*-like zoospores in the cells. (After PASCHER.)

The **Heterocontae** are to be traced back to the Heterochloridales, since their motile cells have the same features (two cilia of unequal length, yellow-green chromatophores, leucosin and oil). *Heterococcus* may be unicellular, or form a flat layer or a short filament. *Tribonema* (*Conferva*) is a widely distributed, fresh-water genus with unbranched filaments (Fig. 320). *Botrydium granulatum* (Fig. 321) is adapted to life on land, occurring on moist loamy soils; the unicellular, but multinucleate thallus has the form of a pear-shaped green balloon, some 2 mm. high, and attached below by branched colourless rhizoids. The zoospores, which are produced in large numbers and escape from an opening at the summit, have two chloroplasts and two unequally long cilia attached at the pointed end (Fig. 321, *B*); on forming a wall they grow into new vesicles. Sexual reproduction is unknown (^{2}).

The most highly developed series of plants derived from the Flagellates is that of the **Isocontae** or **Chlorophyceae**, which are related to the Polyblepharidales. On account of the variety of the forms and the advanced stage of development exhibited, the Chlorophyceae require separate treatment (p. 394). The Diatoms, which also stand in relation to the Flagellatae, must however be considered first.

CLASS IV

Diatomeae (Diatoms) (1, 11, 20, 23)

The Diatomeae (Bacillariophyta) constitute a very large class of unicellular Algae. They occur, usually associated together in large numbers, in both fresh and salt water, and also on damp soil. The subaerial forms can endure dessication for months.

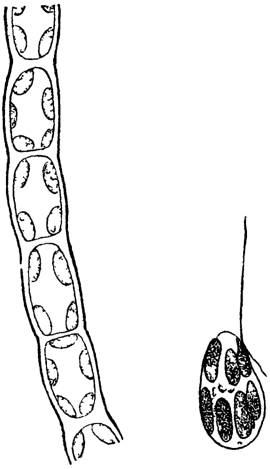

1. 2.

FIG 320 — *Tribonema bombycina* 1, Filament 2, Zoospore With unequally long cilia (After GAY and LUTHER, from OLTMANNS *Algae*)

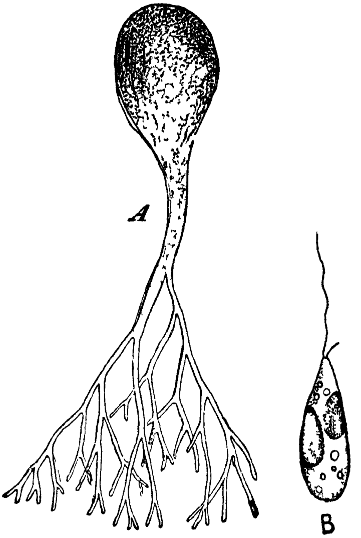


FIG 321 —*Botrydium granulatum* A (×28). B, Zoospore (×1000). (After STRASBURGER and KOLKWITZ)

The cells display a great diversity of shape; this is based either on a bilaterally symmetrical (Fig. 322) or on a centric type (Fig. 323)

The cell-walls, with their outer layers silicified while the inner layers are composed of pectic substance, are very characteristic. The wall is formed of two halves or VALVES, one of which overlaps the other like the lid of a box. The cells thus present two altogether different views, according to the position in which they are observed, whether from the GIRDLE or VALVE SIDE (Fig. 322).

The lateral walls of the two valves are formed of the girdle pieces attached beneath the margins. In some genera the girdle side is extended by the introduction of annular or scale-shaped intermediate bands.

The walls of the cells, particularly on the valve side, are often ornamented with numerous, fine, transverse markings or ribs, and also with small protuberances and pits (Fig. 322, *A*). They are often perforated by open pores which serve to give exit to the mucilaginous secretion.

The two valves are so strongly impregnated with silica that, even when subjected to intense heat, they remain as a siliceous skeleton, retaining the original form and markings of the cell-walls. When the siliceous part is removed by hydrofluoric acid the pectic basis of the wall remains.

The cell has always a central nucleus which is almost as complex in its organisation as in the higher plants. The chromatophores are of a brownish-yellow colour. Pyrenoids are often present. The pigments are chlorophyll and yellow phycoxanthin. Globules of a fatty oil are also included in the cell-contents, and take the place of starch as an assimilation-product.

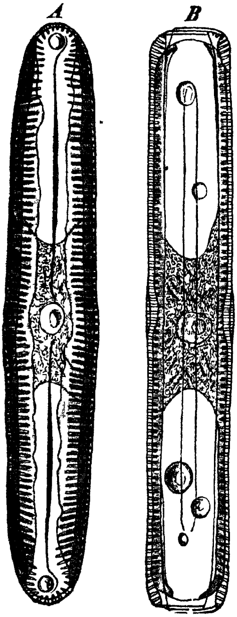


FIG 322.—*Pinnularia viridis*. *A*, Valve view; *B*, girdle view. (× 540. After STRASBURGER.)

The cells are either solitary or form colonies; they are free-floating or united in colonies of various types. Sometimes they are attached by means of gelatinous stalks excreted by the cells themselves (Fig. 324). In other cases the cells remain connected at their angles by mucilage and form bands or zigzag chains, or, on the other hand, they are enclosed in mucilaginous tubes.

The Diatomeae multiply vegetatively by cell-division. In this process the two valves are first pushed apart from one another by the increasing protoplasmic contents of the mother-cell, which then divides longitudinally in such a direction that each of the two new cells retains one valve of the mother-cell. After the division of the protoplasm of the mother-cell is accomplished, each daughter-cell forms, on its naked side, a new valve fitting into the old one. The two valves of a cell are therefore of different ages. In consequence of this peculiar manner of division, since the walls of the cells are silicified and incapable of distension, the daughter-cells become successively smaller and smaller, until finally, after becoming reduced to a definite minimum size, they undergo transformation into AUXOSPORES. The auxospores are usually several times larger than the cells from which they arise, and by their further development they re-establish the original size of the cells. They arise under particular conditions and not necessarily only when the minimal size has been reached.

The sexual reproduction consists of a conjugation of similar gametes, and, so far as is at present known, the reduction-division always takes place in the formation of the sexual cells.

Order 1. Centrales

In these the valves are symmetrical about a centre, and have the sculpturing radially or concentrically arranged (Fig. 323). The great majority of the forms of this order are marine, and play a large part in the composition of the PLANKTON (18). The plankton diatoms are provided with special arrangements for floating, *e.g.* horn-like projections or wings of the cell-wall such as are seen in Figs. 323 and 325. Sometimes they are associated in chains or otherwise by mucilage. The vegetative cells of the Centrales have no motile organs.

Some Centrales are able to form RESTING SPORES within the rigid cell-wall. These sink to the bottom and can survive unfavourable periods, germinating later to form vegetative cells.

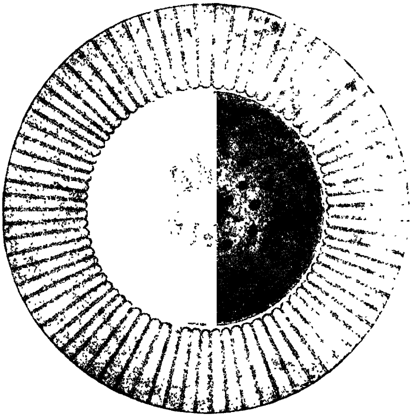


FIG. 323.—*Planktoniella sol.* Atlantic Ocean. A disc-shaped plankton diatom with a hollow wing, serving for floating, arising from the girdle side. The protoplast contains a nucleus and numerous chromatophores. (× 322. After G. KARSTEN.)

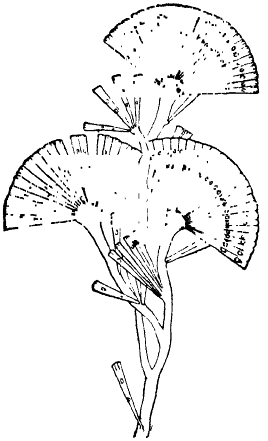


FIG. 324.—*Licmophora flabellata.* Colony of Diatoms with branched gelatinous stalks. (After SMITH, from GOEBEL'S *Organographie.*)

The AUXOSPORE FORMATION in the Centrales takes place by simple growth, by the protoplasmic body of a cell becoming free from the cell-walls and increasing in size; the enlarged cell is first surrounded by a weakly silicified membrane (perizonium), and in this the new valves are formed (Figs. 325, 326, *B*).

In the formation of GAMETES (21), for example in *Biddulphia mobiliensis* (Fig. 326, *C*, *D*), the cell first divide into two gametangia which round themselves off; the contents of each of these divide into numerous (in some species 128) naked nucleated cells. These gametes are provided with a pair of equal cilia (Fig. 326, *E*) and, like the vegetative cells, have the half number of chromosomes. They emerge and fuse in pairs to form naked zygotes with four cilia. These later surround themselves with a wall and have the appearance of small vegetative cells.

Order 2. Pennales

The Pennate Diatoms live mostly on the floor of ponds, etc., or on the surfaces of submerged plants; others inhabit damp soil. In shape they are elongated, elliptical, or boat-shaped, but may be wedge-shaped; the valves have their sculpturing pinnate (Figs. 322, 327). In many of the Pennales (Fig. 322) a longitudinal line corresponding to an opening in the cell-wall, and exhibiting swollen nodules at both extremities and in the middle, is to be seen on the surface of each valve. Forms provided with such a median suture or RAPHE are characterised by peculiar creeping movements, resulting from the friction of the streaming protoplasm in the longitudinal slit of the raphe against the substratum or the surrounding water.

In the process of SEXUAL REPRODUCTION two cells lay themselves side by side and secrete a covering of mucilage. The nucleus of each cell undergoes reduction, dividing to form four haploid nuclei. Four gametes are not, however, produced as might have been expected, but some of the nuclei become small and functionless so that a smaller number of gametes result. Thus in *Navicula*, *Pleurosigma*, etc. the protoplast of each cell divides to form two gametes (Fig. 327), each of which possesses a small functionless nucleus in addition to the larger nucleus that will undergo fusion later. The gametes from the two parent-cells now conjugate in pairs, the zygotes having at first four nuclei; the two large nuclei fuse while the small nuclei degenerate. Each of the diploid zygotes becomes invested by a thin wall (perizonium), within which it undergoes considerable increase in size. Ultimately the protoplast secretes two new valves and thus constitutes a new individual several times larger than the original cells. The zygotes are here—and similarly in all Pennales—at the same time AUXOSPORES and may be termed AUXOZYGOTES.

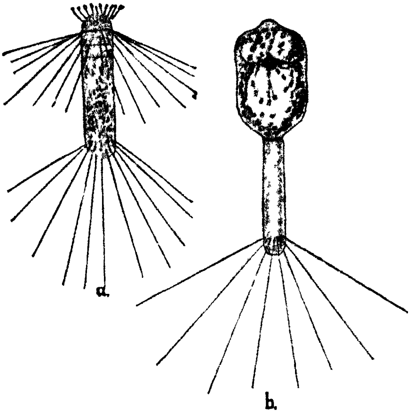


FIG. 325.—*Corethron Valdiviae*. From the Antarctic plankton. *a*, Cell with floating bristles and tentacles; *b*, Auxospore formation; the protoplast after casting off one valve has emerged from the other and, surrounded by the perizonium, has become some four times its original size. (After KARSTEN.)

In other Pennales the process is simpler; thus in some (*Surirella*, *Cocconeis*) each cell forms only one large and three degenerating small nuclei, so that only one zygote is formed on conjugation (Fig. 328). In some (*Rhabdonema*) all gamete-formation is omitted and the protoplast of the mother-cell develops to an auxospore by simple growth.

Many Pennales occur in places where decomposing substances are present in abundance. Such species can assume a saprophytic mode of life, their chromatophores becoming colourless and reduced in size. It has been shown that some colourless species of *Nitzschia* which occur in the sea are exclusively dependent on organic substances for food, the reduction of their chromatophores and pigment being complete (22).

On account of the extreme fineness of the markings of their valves, it is customary to employ certain species of Diatoms as test objects for trying the lenses of microscopes. *Pleurosigma angulatum* is commonly used for this purpose.

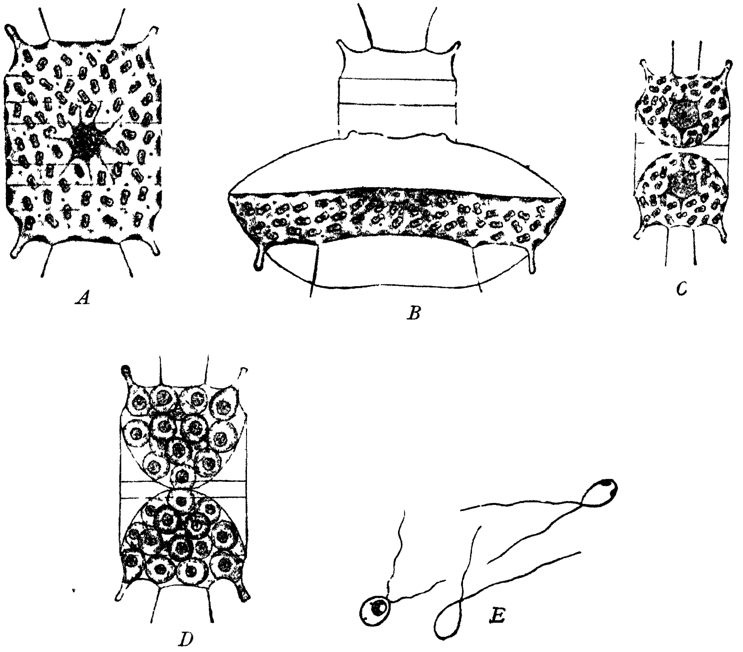


FIG. 326.—*Biddulphia mobiliensis* *A*, View from the girdle side; *B*, auxospore formation; *C*, cell divided into two gametangia, *D*, formation of gametes (*A-D* × 228, after P. BERGON), *E*, gametes of *Coscinodiscus* (after PAVILLARD).

In considering the relationships of the Diatoms the ciliated gametes are of the greatest importance, since they indicate that the Diatoms, and in particular the Centrales, are derived from brown Flagellates.

There is no further development towards higher forms, but the series ends with the Pennales as a phylogenetically younger group derived from the Centrales.

The characteristic structure of the cell-wall, as well as the formation of endogenous spores, and the silicification of the wall, all appear more feebly in some Chrysomonadinae. There are thus indications of special relationship to this group.

Fossil Diatoms are only known as far back as the Upper Lias. They are especially abundant in Tertiary rocks, where their silicified walls form a large part of the deposits of SILICEOUS EARTH (kieselguhr, mountain meal, etc.), and in this form are utilised in the manufacture of dynamite. The Tertiary species are in part identical with those now living or belong to existing genera.

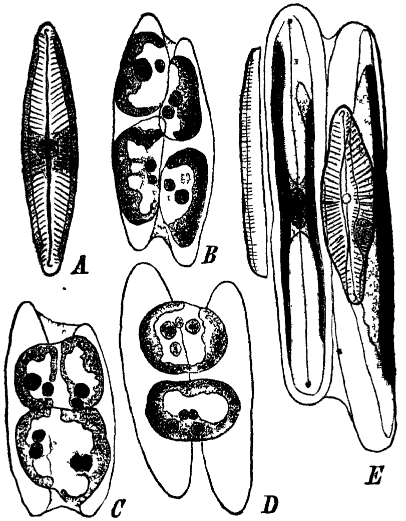


FIG. 327.—Formation of auxozygotes in *Navicula viridula*. *A*, Cell seen from the valve side. *B*, Two cells lying alongside one another; their contents have divided into two daughter-cells, each of which possesses two nuclei. *C*, *D*, Conjugation in pairs of the daughter-cells to form the auxospores, which at first contain four nuclei. *F*, The two full-grown auxospores. (× 500. After KARSTEN.)

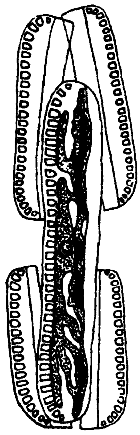


FIG 328.—*Surirella saxonica*. Auxozygote in the empty valves of the parent-cells. (After G. KARSTEN.)

The two orders of Diatomeae are mainly distinguished by the following characters:—

Centrales.—Cells centric, without raphe, non-motile; auxospore formation independent of the sexual fusion; gametes ciliated.

Pennales.—Cells bilateral, sometimes with raphe, motile; auxospore formation in connection with the conjugation of non-motile gametes.

CLASS V

Chlorophyceae (Green Algae) (1, 11, 28 38)

The pure green chloroplasts, which frequently contain pyrenoids and nearly always form starch, are characteristic of the Chlorophyceae. The cell-walls consist mainly of cellulose. The asexual reproduction in all typical cases is by means of naked swarm-spores (zoospores);

these are pear-shaped, with two or four equal cilia at the pointed end, usually a red eye-spot, and in the hinder part a curved or bowl-shaped chloroplast.

The swarm-spores by means of phototactic movements (p. 330) reach situations which provide favourable conditions for their germination, and grow into new plants.

In the sexual reproduction (Figs. 329, 331) two gametes, which often resemble the asexual swarm-spores, conjugate; the male gametes at least are always ciliated; the female are in some cases non-motile egg-cells. The spherical zygote usually becomes a thick-walled resting cell and is often coloured red by haematochrome (= carotin). On its germination the reduction-division takes place.

Most Chlorophyceae occur, free or attached, in fresh water, or in moist situations; some kinds are aerophilous and can endure complete drying-up (28a). A few live symbiotically in Lichens or within the cells of lower animals. Some larger forms occur on the sea-coast. The Chlorophyceae, on the other hand, form a very small proportion of the marine plankton.

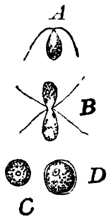


FIG. 329.—*Haematococcus Butschlii*. *A*, gamete; *B*, conjugation of two gametes; *C*, *D*, zygotes. (×800. After BLOCHMANN.)

Order 1. Volvocales

Typical representatives of this order are characterised by the cilia being retained by their cells in the vegetative stage; the plants are therefore motile. Each cell has a nucleus and a chloroplast. They are widely distributed organisms of the fresh-water plankton, and may appear in such numbers as to give the water a green colour. Their development is often favoured by organic food materials; a few species (*e.g. Polytoma uvella*) can even live as total saprophytes and have no chlorophyll. All Volvocales have cell-walls which, according to the species and stage of development, may contain hemicelluloses, pentoses, pectin, and true cellulose.

Chlamydomonas, belonging to the family **Chlamydomonaceae** (29a), is a widely distributed genus. The free-swimming microscopically small cells (Fig. 330) have two cilia, a red eye-spot, two contractile vacuoles, and a cup-shaped chloroplast with a pyrenoid. Asexual reproduction is by means of swarm-spores which are produced by the longitudinal division of the cell-contents to form 2-16 cells, which become free by the rupture of the original cell-wall. There is also a process of sexual reproduction. Biciliate gametes arise in much larger numbers (2-64 or more) in the mother-cell, and these unite in pairs by their anterior ends to form the zygote (Fig. 329). Besides species with isogamy there are others that are heterogamous; in these a small (male) gamete fuses with a larger (female) cell (Fig. 331). The male and female cells here always arise from different mother-cells, and the same holds for the gametes of some isogamous forms. A further stage is seen in *Chlamydomonas coccifera*, in which the female gamete has no cilia and is thus an egg-cell. Thus, in this genus of unicellular Algae, a series leading from isogamy to oogamy can be traced.

Haematococcus is closely related to *Chlamydomonas* ; the cells contain haematochrome and give rise to the red colour of rain puddles (*H. pluvialis*) and to red snow (*H. nivalis*).

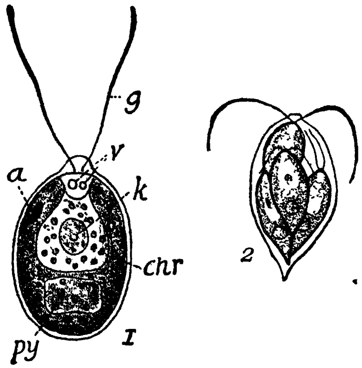


FIG. 330. — *1*, *Chlamydomonas angulosa* (after DILL); *g*, cilia ; *v*, vacuole, *k*, nucleus, *chr*, chromatophores ; *py*, pyrenoid ; *a*, eye-spot. *2*, *Chl. subcaudata*, with four daughter-cells in a parent-cell (from PASCHER).

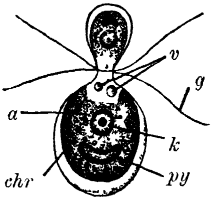


FIG. 331 —*Chlamydomonas Braunii.* Fusion of a male with a female gamete. Lettering as in Fig. 330. (After GOROSCHANKIN.)

The Family **Volvocaceae** (^{30}), including colonial forms, is closely connected to the unicellular Chlamydomonads. In *Pandorina* 16, and in *Eudorina* 32, cells are united to form free-swimming, spherical colonies. In asexual reproduction each cell of the colony divides into a corresponding number (16 or 32) of cells, which do not separate, but are set free as complete daughter-colonies. In *Volvox* (Fig. 332) the hollow spheres, as large as a pin-head, are composed of several thousand cells, each with two cilia, an eye-spot, and a chloroplast; the protoplasts are connected by fine processes, and, since further there is a certain division of labour between them, the spherical organism must be regarded as a multicellular individual and not a mere colony. In the asexual reproduction only certain cells divide to form new individuals and these project into the interior of the parent sphere ; they become detached, lying within the central cavity (Fig. 332, *E*), and only become free by the breaking down of the parent individual. The sexual cells of *Volvox* are differentiated as egg-cells and spermatozoids. The egg-cells arise by the enlargement of single cells of the colony ; they are large, green, non-motile cells surrounded by a mucilaginous wall. The small spermatozoids are elongated bodies of a bright yellow colour, provided with two cilia attached laterally below the colourless anterior end ; they arise by the division of a cell of the colony into numerous daughter-cells. After fusing with a spermatozoid within the cavity of the colony, the egg-cell is transformed into the thick-walled, resting oospore, on the germination of which the reduction in number of chromosomes takes place. Since the cells which are not transformed into reproductive cells die and break down, *Volvox* provides the first example of the regular occurrence of a dead body or "corpse." Oogamy is also met with in *Eudorina*, while *Pandorina* is isogamous. Since, in the latter, only gametes from different colonies fuse, the morphologically similar colonies show a certain physiological sexual difference.

The Volvocales form a series ending with *Volvox*, and do not lead to any higher orders of the Algae.

Order 2. Protococcales

The cells of the Protococcales are distinguished from those of the Volvocales by having no cilia in the vegetative condition, so that they are non-motile (Fig. 333).

They have a chloroplast and usually a single nucleus. Reproduction is by means of zoospores, in place of which, however, in many genera non-ciliated aplanospores are found (Fig. 334). Sexual reproduction is by the fusion of ciliated isogametes, or less commonly heterogametes ; oogamy does not occur. Sexuality has only been demonstrated in certain genera and appears not to have arisen in the simpler forms.

The Protococcales occur mainly in fresh water ; some (*e.g.*, *Pleurococcus*) form, along with other Algae, a regular constituent of the green growth on the bark of trees and on walls (28a). Others occur as symbionts in Lichens and even in the protoplasm of lower animals (*Chlorella vulgaris*, in Infusoria, *Hydra*, etc.).

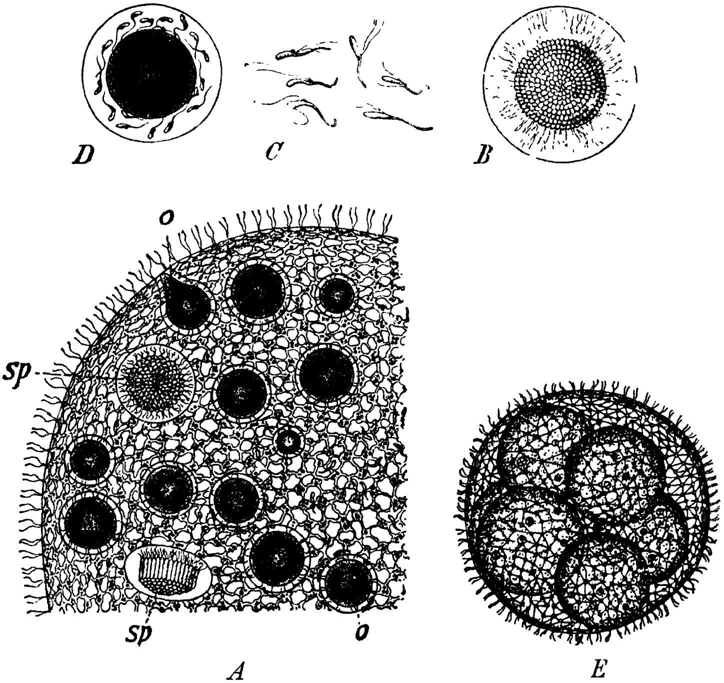


FIG. 332.—*Volvox globator*. *A*, Portion of a colony with egg-cells (*o*), and groups of spermatozoids (*sp*) (×165). *B*, Bundle of spermatozoids derived by the division of a cell (×530). *C*, Spermatozoids (×530). *D*, Egg-cell surrounded by spermatozoids in the mucilaginous membrane. (×265. After F. COHN.) *E*. *Volvox aureus*. Sphere enclosing young daughter individuals. (After KLEIN.)

As in the Volvocales there is an ascending series from unicellular forms to colonies of cells. *Chlorococcum* (Fig. 333) and *Chlorella* (Fig. 334) (31, 32) are examples of the former. *Scenedesmus*, which is widely spread in fresh water, forms simple colonies of usually four cells united in a row (Fig. 335). Each of the cells divides in the direction of its length to form four non-ciliated cells with cell-walls ; these on becoming free from the wall of the parent-cell constitute a new colony.

More complicated cell-colonies are met with in *Pediastrum* (Fig. 336), in the form of a free-floating plate. The formation of asexual swarm-spores is effected by the division of the contents of a cell into a number (in the case of the species illustrated, *P. granulatum*, into 16) of naked swarm-spores, each with two cilia. On escaping through the ruptured cell-wall (Fig. 336 *A*, *b*), these are enclosed in a mucilaginous envelope. After moving about vigorously within this envelope, they eventually collect together and form a new colony. *Pediastrum* has also a method of sexual reproduction by isogametes.

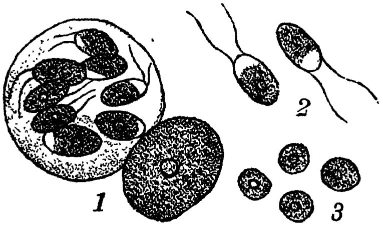


FIG. 333.—*Chlorococcum* (*Chlorosphaera*) *limicola*. *1*, Vegetative cell and cell divided into 8 zoospores; *2*, free zoospores; *3*, zoospores after they have formed cell-walls. (After BEYERINCK, from OLTMANNS' *Algae*.)

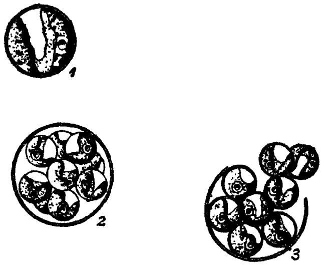


FIG. 334.—*Chlorella vulgaris*. *1*, Cell; *2*, *3*, division into eight aplanospores. (After GRINTZESCO.)

The life-history of the Water-net (*Hydrodictyon utriculatum*) is essentially similar. It is one of the most beautiful of the free-floating, fresh-water Algae, the hollow colonies being formed of elongated, cylindrical, multinucleated cells united together to form a many-meshed net, which may be 20 cm. in length. In the old cells of the net a large number of zoospores are formed, which are not set free, but arrange themselves within the parent-cell to form a new net, losing their cilia and becoming enclosed by cell-walls. The daughter-net is set free by the dissolution of the wall of the parent-cell.

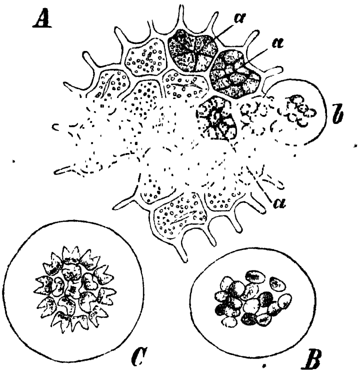


FIG. 336.—*Pediastrum granulatum*. *A*, An old cell-family: *a*, cells containing spores; *b*, spores in process of extrusion (the other cells have already discharged their swarm-spores). *B*, Cell-family shortly after extrusion of the spores. *C*, Cell-family 4½ hours later. (× 300. After AL. BRAUN.)

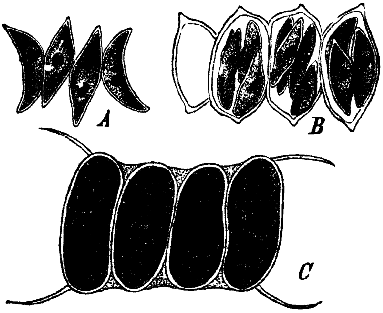


FIG. 335.—*A*, *Scenedesmus acutus*. *B*, The same, undergoing division. *C*, *Scenedesmus caudatus*. (× 1000. After SENN.)

The Protococcales like the Volvocales can be derived from the Flagellata. In contrast to the latter group the non-motile, non-ciliated condition of the cells has become prevalent as it has throughout the higher Algae. In some genera of the

Protococcales even the spores do not develop cilia, although, as a rule, the reproductive cells of the Algae tend to retain the Flagellate character. The loss of motility is accompanied by a more complex external form of the cells.

Order 3. Ulotrichales

The Ulotrichales exhibit, as compared with the unicellular green Algae, an advance in the external segmentation of the thallus. It is always multicellular, and, in most of the genera, consists of simple or branched filaments. The filaments are either attached by a colourless basal cell to the substratum (Fig. 338 *A*) or float free. The thallus of the marine genus *Ulva* (*Ulva lactuca*, SEA LETTUCE) has the form of a large, leaf-like cell surface, and is two layers of cells thick (Fig. 78, young plant). In *Enteromorpha* (Fig. 337) the thallus is ribbon-shaped, either cylindrical or flattened ; when young it is two-layered, but later it becomes hollow, the wall thus consisting of one layer of cells.

The majority of the Ulotrichales live in fresh or salt water ; a few aerial forms (**Chroolepideae**) grow on stones, trunks of trees, and, in the tropics, on leaves. To this family belongs *Trentepohlia* (or *Chroolepus*) *Jolithus*, often found growing on stones in mountainous regions. The cell-filaments of this species appear red on account of the haematochrome they contain, and possess a violet-like odour.

The cells have always only one nucleus and also a single chloroplast. The asexual reproduction is accomplished by the formation of ciliated swarm-spores. Sexual reproduction is effected either by the fusion of planogametes, or the sexual cells are differentiated as non-motile egg-cells and motile spermatozoids.

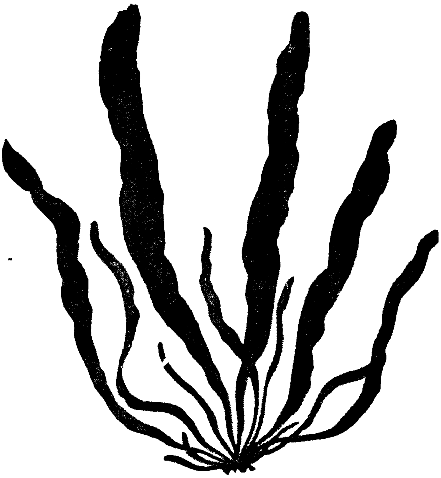


FIG. 337.—*Enteromorpha compressa*, a common marine Alga. (½ nat. size.)

Ulothrix zonata (Fig. 338 *A*), the typical representative of the group, is one of the commonest filamentous Algae. The filaments of *Ulothrix* exhibit no pronounced apical growth ; they are unbranched, attached by a rhizoid-cell, and consist of rows of short cells ; each cell contains a band-shaped chloroplast arranged like an open ring round the middle of the cell. The asexual reproduction is effected by means of swarm-spores, which have four cilia (*C*), and are formed singly or by division in a cell of the filament (sporangium). The swarm-spores escape through a lateral opening (*B*) formed by absorption of the cell-wall, and, after swarming, give rise to new filaments. The sexual swarm-cells, or isogametes, are formed in a similar manner by the division of the cells, but in much greater numbers. They are also smaller, and have only two cilia (*D*, *E*). In other respects they resemble the swarm-spores, and possess a red eye-spot and one chromatophore. By their conjugation in pairs, zygotes (*F-H*) are produced, which, after drawing in their cilia, round themselves off and become invested with a cell-wall. After a shorter or longer period of rest the zygotes are converted into unicellular germ plants (*J*), and give rise to several aplanospores (*K*), which in turn grow out into new filaments. Under some conditions the gametes can give rise to new plants parthenogenetically without conjugating. *Ulva* and *Enteromorpha* are also isogamous (^{33a}), the former being dioecious.

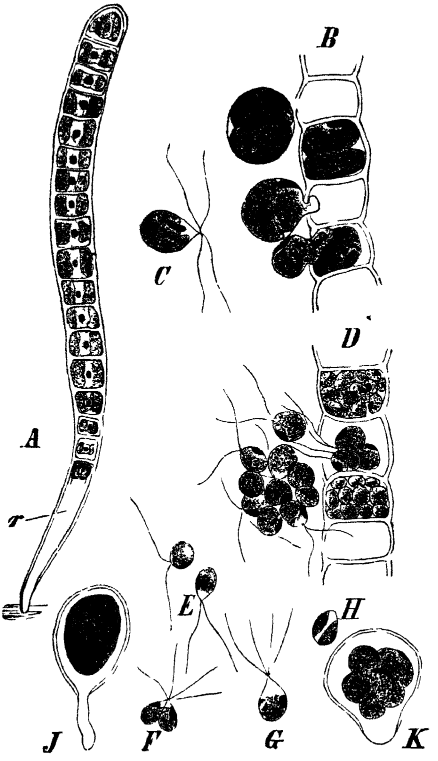


FIG. 338.—*Ulothrix zonata*. *A*, Young filament with rhizoid-cell *r* (× 300); *B*, portion of filament with escaping swarm-spores; *C*, single swarm-spore; *D*, formation and escape of gametes; *E*, gametes; *F*, *G*, conjugation of two gametes; *H*, zygote; *J*, zygote after period of rest; *K*, zygote after division into swarm-spores. (*B*-*K* × 482. After DODEL.)

The genus *Oedogonium* (^{34}) with unbranched filaments may be cited as an example of the oogamous Ulotrichales. The asexual swarm-spores of *Oedogonium* are unusually large, and have a circlet of cilia around their colourless, anterior extremity (Fig. 339 *B*). In this case the swarm-spores are formed singly, from the whole contents of any cell of the filament (*A*), and escape by the rupture of the cell-wall. After becoming attached by the colourless end they germinate, giving rise to a new filament. For the purpose of sexual reproduction, on the other hand, special cells become swollen and differentiated into barrel-shaped oogonia. A single large egg-cell with a colourless receptive spot is formed in each oogonium by the contraction of its protoplasm, while the wall of the oogonium becomes perforated by an opening at a point opposite the receptive spot of the egg. At the same time, other, generally shorter, cells of the same or another filament become converted into antheridia. Each antheridium usually gives rise to two spermatozoids. The spermatozoids are smaller than the asexual swarm-spores, but have a similar circlet of cilia. They penetrate the opening in the oogonium and one fuses with the egg-cell, which then becomes transformed into a large firm-walled oospore. On the germination of the oospore its contents become divided into four swarm-spores, each of which gives rise to a new filament.

In some species of *Oedogonium* the process of sexual reproduction is more complicated. Spermatozoid-like swarm-spores (androspores) emerge from the antheridia. They are not, however, capable of effecting fertilisation themselves, but become attached to female filaments and develop into small plants consisting of few cells, the so-called "dwarf-males." The actual spermatozoids are produced from the upper cells of these (Fig. 339 *C*, *D*).

The genus *Coleochaete* (Fig. 340) exhibits the highest development of the sexual reproductive organs among the Green Algae. The long colourless neck of the flask-shaped oogonium opens at the tip to allow of the entrance of the spermatozoid. The spherical oospore increases in size and becomes surrounded by a single layer of pseudo-parenchymatous tissue derived from filaments that spring from the stalk-cell of the oogonium and neighbouring cells. In this way a fruit-like body is formed (Fig. 340, 4). On germination the oospore undergoes a reduction-division and divides into 16-32 wedge-shaped cells, then breaks up and liberates a swarm-spore from each cell. The spherical, biciliate spermatozoids are formed singly in small, terminal antheridia (Fig. 340, 1). The asexual reproduction is by biciliate zoospores formed singly in cells of the thallus.

Order 4. Siphonocladiales

The algae of this order are filamentous and usually branched; they are distinguished from the Ulotrichales by their large multinucleate cells (Figs. 7, 9), the chloroplasts of which are either solitary, large, and reticulately-formed (Fig. 9), or appear as numerous small discs. It may be assumed that the Siphonocladiales are derived from Algae resembling *Ulothrix* by enlargement of the cells of the filament, increase in number of the nuclei, and alteration of the chromatophore.

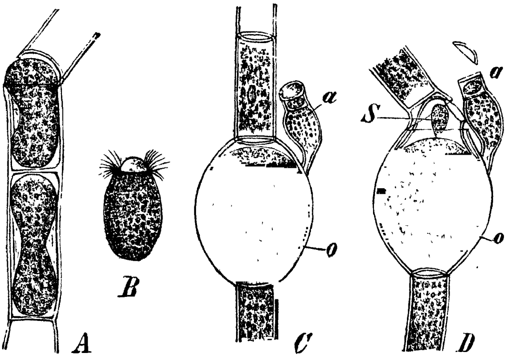


FIG. 339.—*A*, *B*, *Oedogonium*: *A*, escaping swarm-spores; *B*, free swarm-spore. *C*, *D*, *Oedogonium ciliatum*: *C*, before fertilisation; *D*, in process of fertilisation; *o*, oogonia; *a*, dwarf-males; *S*, spermatozoid. (× 350. After PRINGSHEIM.)

The genus *Cladophora* (Fig. 341), numerous species of which occur in the sea and in fresh water, is one of the most important representatives of the order. *Cl. glomerata* (Fig. 81) is one of the commonest algae in streams, often attaining the length of a foot. It is attached by rhizoid-like cells, and consists of branched filaments with typical apical growth, which some other representatives of the order do not show. The structure of the cells is represented in Figs. 7, 9, and 17. Branching takes place from the upper ends of the cells by the formation of a protrusion which is cut off as the first cell of the branch. Asexual reproduction is by means of biciliate zoospores (Fig. 341), or, in marine species, tetraciliate zoospores, which arise in numbers from the upper cells of the filaments, and escape from these sporangia by a lateral opening in the wall. The sexual reproduction is isogamous.

Only in the genus *Sphaeroplea* has the sexual reproduction become oogamous. *S. annulina* consists of simple filaments and occurs in fresh water.

Many forms occur in the sea (*e.g. Siphonocladus*), and some have a highly complicated thallus, which is always, however, formed of branched filaments; by calcareous incrustation some forms come to resemble coral. *Acetabularia mediterranea* (Fig. 342) will serve as an example of such calcareous Algae. The thin stalk of the thallus is attached by means of rhizoids, while the umbrella-like disc consists of closely united tubular outgrowths, each of which is to be regarded as a gametangium.

Order 5. Siphonales

The Siphoneae are mainly marine, though some occur in fresh water. They are distinguished from the preceding groups of Algae by the structure of their thallus, which, although more or less profusely branched, is not at first divided by transverse septa. The cell-wall thus encloses a continuous protoplasmic body in which numerous nuclei and small green chloroplasts are embedded. Only the reproductive organs are divided off by septa. The Siphonales may be derived from the Siphonocladiales by assuming that the capacity of forming transverse walls in some representatives of the latter was lost in the phylogeny.

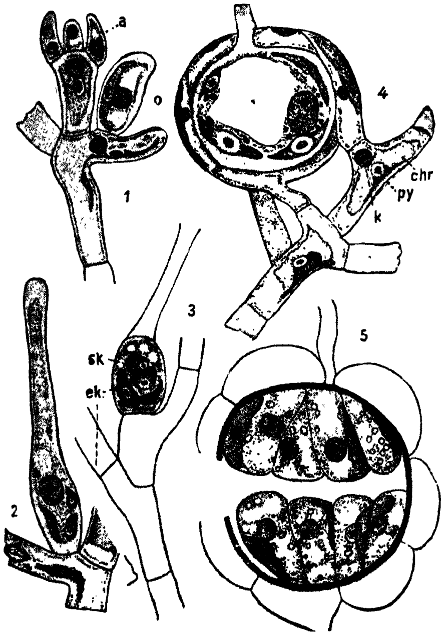


FIG. 340.—*Coleochaete pulvinata*. *1*, Antheridium (*a*) and young oogonim (*o*). *2*, Oogonium shortly before opening. *3*, Fertilised oogonium; *ek*, nucleus of the ovum; *sk*, male nucleus. *4*, Oospore enclosed to form the "fructification." *5*, Germinating oospore. (After OLTMANNS.)

Vaucheria occurs commonly in fresh water or on damp soil. The thallus consists of a single branched filamentous cell attached to the substratum by means of colourless rhizoids (Fig. 344.) The thallus in most other Siphoneae is, on the other hand, a specialised branch-system. The genus *Bryopsis* has a delicate, pinnately-branched thallus (37). In *Caulerpa prolifera* (Fig. 343), which occurs in the Mediterranean, the lobes of the thallus (assimilators) are leaf-like and are frequently proliferous. They spring from a colourless, creeping main axis, which has continued apical growth and sends colourless rhizoids into the soil (37). In other species they are pinnately lobed or branched. The whole thallus, encloses but one cell-cavity, which is, however, often traversed by a network of cross-supports or trabeculae. Starch-forming leucoplasts are present in the colourless parts of the thallus.

Some species of *Vaucheria* become incrusted with lime and may lead to the formation of calcareous tufa. Some other genera (*e.g. Halimeda,* which occurs in the warmer seas) are regularly calcified.

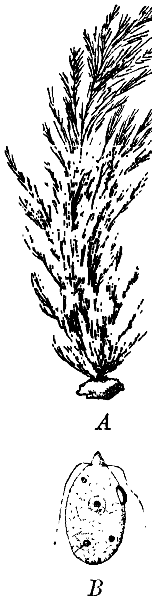


FIG. 341.—*A*, *Cladophora.* General habit (reduced). *B*, *Cladophora glomerata.* Swarm-spore. (×500. After STRASBURGER.)

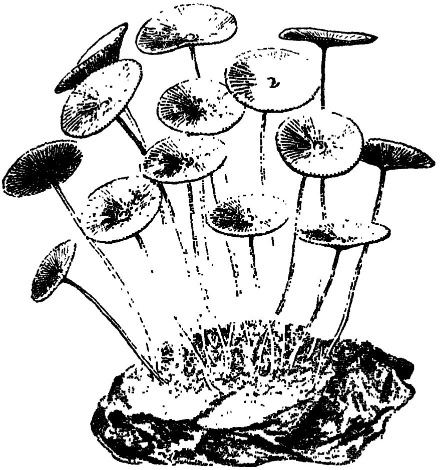


FIG. 342.—*Acetabularia mediterranea.* (Nat. size. After OLTMANNS.)

Besides an asexual reproduction by means of zoospores the Siphonales have sexual reproduction. This is either heterogamous (*e.g. Bryopsis*) or oogamous. Isogamy does not occur.

The asexual swarm-spores of *Vaucheria,* which differ from those of the other Siphonales, are developed in special sporangia, cut off from the swollen extremities of branches by means of transverse walls (Fig. 344). The whole contents of such a sporangium become converted into a single green swarm-spore. The wall of the sporangium then ruptures at the apex, and the swarm-spore, rotating on its longitudinal axis, forces its way through the opening. The swarm-spore is so large as to be visible to the naked eye, and contains numerous nuclei embedded in a peripheral layer of colourless protoplasm. It is entirely surrounded by cilia, which protrude in pairs, one pair opposite each nucleus. Morphologically the swarm-spores of *Vaucheria* correspond to the total mass of individual zoospores of an ordinary sporangium.

The sexual reproduction of *Vaucheria* is not effected, like that of the other Siphoneae, by the conjugation of motile gametes, from which, however, as the earlier form of reproduction, it may be considered to have been derived. The oogonia and antheridia first appear as small protuberances, which grow out into short lateral branches, and become separated by means of septa from the rest of the thallus (Fig. 345 *o*, *a*). At first, the rudiment of an oogonium contains numerous nuclei, of which all but one, the nucleus of the future egg-cell, retreat again into the main filament before the formation of the septum. In its mature condition the oogonium has on one side a beak-like projection containing only colourless protoplasm. The oogonium opens at this place, the oosphere rounding itself off. The antheridia, which are also multinucleate, are more or less coiled (*a*), and open at the tip to set free their mucilaginous contents, from which the numerous swarming spermatozoids become free. The spermatozoids are very small, and have a single nucleus and two cilia inserted on one side. They collect around the receptive spot of the egg-cell, into which one spermatozoid finally penetrates. After the egg-cell has been fertilised by the fusion of its nucleus with that of the spermatozoid, it becomes invested with a wall and converted into a resting oospore. On germination the oospore grows into a filamentous thallus.

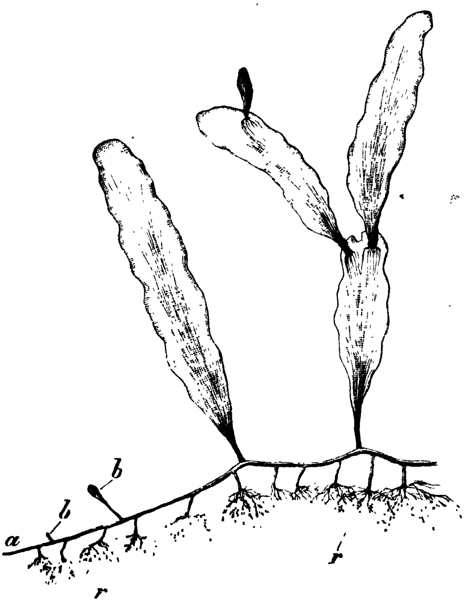


FIG. 343.—*Caulerpa prolifera.* The shaded lines on the lobes of the thallus indicate the currents of protoplasmic movement. *a*, Growing apex of the thallus axis; *b*, *b*, young thallus lobes; *r*, rhizoids. (½ nat. size.)

The Chlorophyceae appear to be a natural group of plants that can be directly connected with the Flagellates. They either resemble the latter throughout their whole developmental cycle, or they at least recall their Flagellate ancestry by the form of their naked, motile, reproductive cells. This is brought out especially clearly by the fact that the zoospores of some Chlorophyceae can shed their cilia and become amoeboid; they then creep about by means of pseudopodia, and can feed like animals on various minute organisms. There are several ascending series within the Chlorophyceae which exhibit progressions from simple to more highly differentiated forms. This is particularly clear in the Volvocales where, starting from unicellular forms, multicellular colonies with equivalent, unconnected cells, that can all serve for vegetative life and for reproduction, lead on to multicellular individuals with pronounced division of labour between their cells. As regards the sexual reproduction, progressive differentiation can also be followed. The lowest stage is that of isogamy, in which the conjugating gametes may even proceed from the same parent-cell. This leads by way of heterogamy to the simpler cases of oogamy; in the higher types of oogamy the egg is not liberated but is fertilised in the oogonium. The case of *Coleochaete* is especially noteworthy, for in it fertilisation acts as a stimulus on the cells of the branch bearing the oogonium, so that a primitive type of "fruit-formation" results.

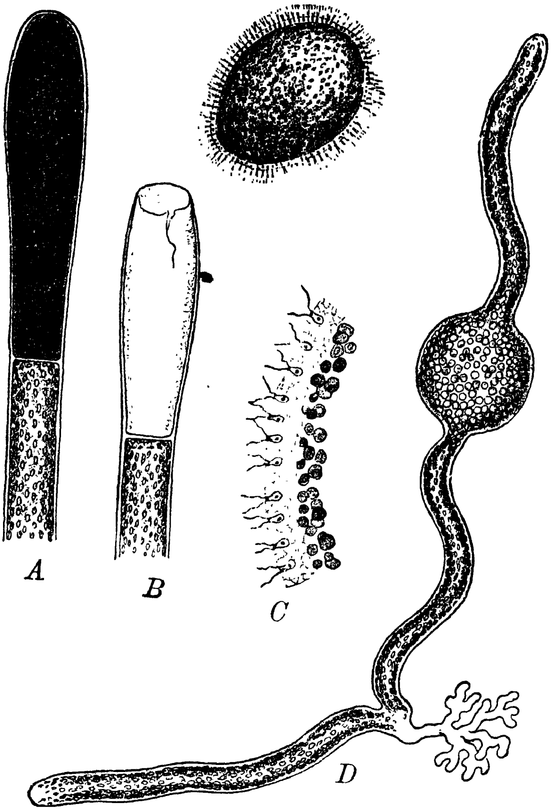


FIG. 344.—*Vaucheria sessilis*. *A*, Young sporangium. *B*, Zoospore with the sporangium from which it has escaped. *C*, A portion of the peripheral zone of a zoospore. *D*, A young plant with rhizoids developed from a zoospore. (*A*, *B* after GÖTZ; *D* after SACHS; from OLTMANNS' *Algae*. *C* after STRASBURGER.)

The reduction-division takes place very generally on the germination of the zygote, so that the plant throughout its whole development is haploid.

The Green Algae are without doubt a very ancient group of lower plants. Only the marine Siphonocladiales, in which the thallus is rendered more resistant by calcification, can be followed back with certainty to the Silurian. These calcareous algae played an especially important part in Triassic times and were present in great variety.

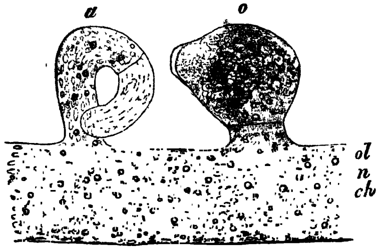


Fig. 345.—*Vaucheria sessilis.* Portion of a filament with an oogonium, *o* ; antheridium, *a* ; *ch*, chromatophores ; *n*, cell nuclei ; *ol*, oil globules. (× 240. After Strasburger.)

The following characters may be used to distinguish the Orders :

Volvocales. Unicellular or multicellular, always motile even in the vegetative condition.

Protococcales. Unicellular or multicellular, non-motile in the vegetative condition, no cell-filaments.

Ulotrichales. Cell-filaments or more highly organised thalli, cells uninucleate.

Siphonocladiales. Cell-filaments or more highly organised thalli, cells multinucleate.

Siphonales. Cells tubular, without transverse septa, multinucleate.

Class VI

Conjugatae (1, 11, 24-26)

The Conjugatae are pure green algae with uninucleate cells, but, in contrast to the Chlorophyceae, have neither zoospores nor ciliated gametes (Acontae). In their sexual reproduction there is a conjugation of two similar non-motile gametes to form a zygote ; the gamete in almost all cases is derived from the whole protoplast of a vegetative cell. After a prolonged resting period the zygote undergoes reduction-division and germinates ; thus the Conjugatae, like the Chlorophyceae, are haploid organisms.

The Conjugatae are a varied group of fresh-water algae. They are either unicellular (Desmidiacae) or have the form of unattached, unbranched filaments (Zygnemaceae).

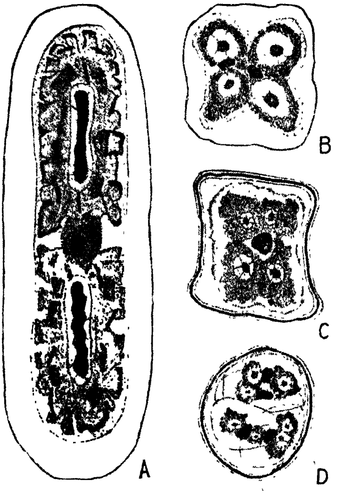


Fig. 346.—*A*, *Cylindrocystis Brebisonii* ; the nucleus is in the centre between two large lobed chloroplasts with elongated pyrenoids. *B*, The zygote before, and *C*, after the fusion of the nuclei. *D*, The zygote before germination, with four daughter-cells. (After Kauffmann.)

The **Desmidiaceae** (24, 25), which occur especially on peat-moors where the water has an acid reaction (24 a), are among the most beautiful of algae and exhibit a great variety in form.

Their cells may be cylindrical (*Cylindrocystis*, Fig. 346), or semilunar (*Closterium*, Fig. 348) ; they are often constricted in the middle and biscuit-shaped

(*Cosmarium*, Fig. 347 *B*), or stellate (*Micrasterias*. Fig. 347 *D*). Chains of cells occur—in addition to the types with solitary cells.

In most cases the wall is composed of two halves, the bevelled edges of which overlap at the middle line of the cell. It is only in a few genera (which are grouped in a special Family, the Mesotaeniaceae) that the wall is not thus constructed of two halves. The wall consists of an inner layer of cellulose and an outer thin "cuticular" layer. It is frequently provided with spiny or warty projections, and is usually perforated by pores. Within each of the two symmetrical halves of the cell there is a green chloroplast with one or several

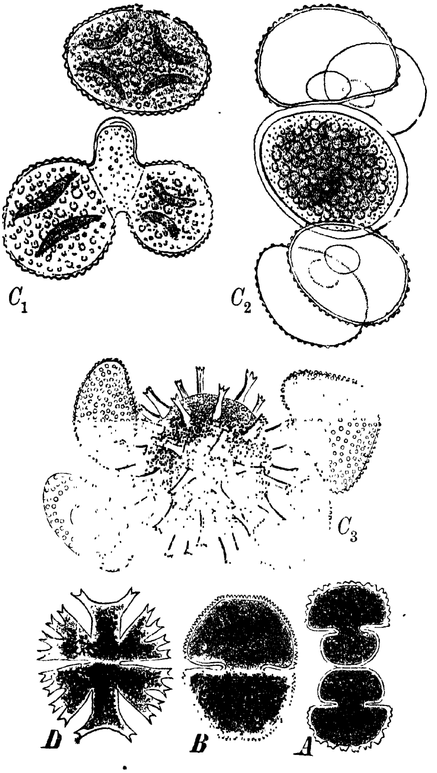


FIG. 347.—*A*, *Cosmarium coelatum*, dividing. *B*, *C*, *Cosmarium botrytis*. C_1, Two cells at right angles preparing for conjugation—the lower cell shows the conjugation canal; C_2, gametes fused into the young zygote; C_3, mature zygote; *D*, *Micrasterias crux melitensis*. (After RALFS; C_2, C_3 after DE BARY.)

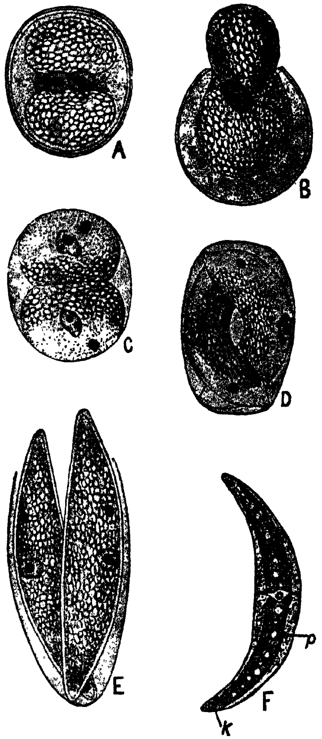


FIG. 348.—*Closterium*. *A*, Zygote before germination showing the two nuclei not yet united; *B*, germinating zygote with the nuclei united; *C*, division into two cells each containing one larger and one smaller nucleus; *D*, further state of germination; *E*, young plants escaping from the cell-membrane; *F*, *Closterium moniliferum*, mature plant. (*A-E* after KLEBAHN.)

pyrenoids ; the nucleus occupies a middle position (Fig. 346 *A*). The chloroplasts exhibit considerable variety in form, *e.g.* they are lobed in *Cylindrocystis*, while in *Closterium* the shape is that of a cone with longitudinal ridges, so that the cross-section is stellate.

Some Desmidiaceae exhibit phototactic movements ; these are effected by the agency of mucilaginous threads emerging from the pores in the cell-wall.

Multiplication is effected by cell-division. This is accomplished by the formation of a partition wall across the middle of the cell, after the nuclear division is completed. Each daughter-cell eventually attains the size and form of the mother-cell, by the outgrowth of a new half on the side towards the plane of division (Fig. 347 *A*).

In conjugation two cells approach each other, and surround themselves with a mucilaginous envelope. Their cell-walls rupture at the constriction, the protoplasts pass into the conjugation canal, which soon becomes mucilaginous, and then unite to form a zygospore. The zygospores frequently present a very characteristic appearance, as their walls are often beset with spines (Fig. 347 C_3). The four empty cell-halves may be seen close to the spore.

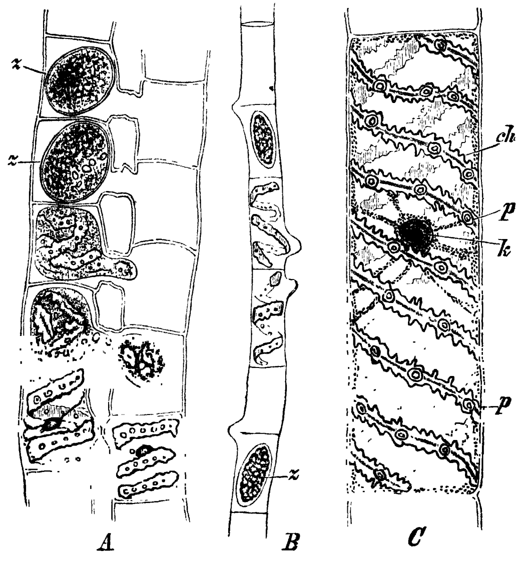


FIG. 349.—*A*, Conjugation of *Spirogyra quinina* (× 240). *B*, *Spirogyra longata* (× 150); *z*, zygospore. *C*, Cell of *Spirogyra jugalis* ; *k*, nucleus ; *ch*, chromatophores ; *p*, pyrenoid (× 256).

The two sexual nuclei in the zygote do not fuse until germination of the latter is about to commence (Figs. 346 *B*, *C* ; 348 *A*, *B*). The resulting nucleus then undergoes division, with reduction, into four nuclei. In *Cylindrocystis* four uninucleate young individual cells result. In most Desmidiaceae, however, only two cells are formed from the zygote, each of which has thus two nuclei of different sizes ; the smaller nuclei degenerate and disappear (Fig. 348). In *Hyalotheca*, the cells of which are united in chains, three of the four nuclei degenerate, so that only a single young cell results.

The **Zygnemaceae**, (26) with unbranched filaments, include the well-known genus *Spirogyra*, the numerous species of which occur in still water as free-floating tangled masses, especially in the spring. The filaments grow in length by the transverse division and elongation of all the cells. The transverse septum, which is composed of cellulose, usually becomes split, as in the Desmidiaceae ; the cells are then held together only by the delicate "cuticular" layer that forms a sheath to the whole filament. Thus the filaments readily break up into portions, or into the single cells, which can then continue to grow and divide. The cell-wall is smooth and without pores. Each cell has a single nucleus and one or several chloroplasts with pyrenoids (Fig. 349 *C*) ; the chloroplasts have the form of spiral bands lying against the inside of the wall. In the genus *Zygnema* each cell has two stellate chloroplasts ; in *Mesocarpus* there is an axil plate-shaped chloroplast. The filaments have a certain power of movement, the cause of which is uncertain.

When conjugation is about to take place two sexually different filaments become parallel and closely appressed. Along the line of contact papillae project from the cells, so that the filaments undergo a secondary separation and have a ladder-like appearance (Fig. 349 *A*) When the tips of the papillae are in contact they become mucilaginous, so that a continuous conjugation-canal results. Through this the protoplast of the male cell passes as the male gamete into the corresponding female cell and the two protoplasts fuse ; the resulting zygospore rounds itself off, becomes thick-walled, and is densely filled with fat and reddish-brown spheres of mucilage. The chloroplasts of the male cell break down. On the germination of the zygote the fusion nucleus undergoes reduction-division with the production of four haploid nuclei ; one of these becomes the nucleus of the first cell of the young plant, while the three others degenerate (Fig. 350). Thus only one young plant is produced from the zygote, and by its elongation and cell-division gives rise to a filament.

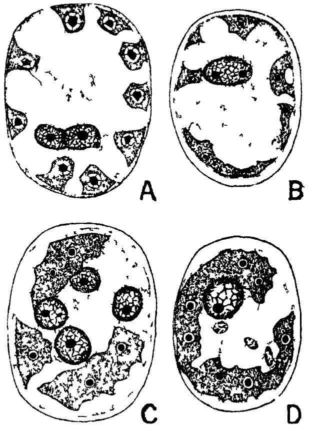


FIG. 350 —*Spirogyra longata* : zygotes of various age. *A*, The two sexual nuclei before fusion ; *B*, after fusion ; *C*, division of the nucleus of the zygote into four haploid nuclei ; *D*, the three small nuclei degenerating. The chloroplasts are represented as in optical section. (After TRONDLE.)

If, as is commonly the case, the filaments are of different sex, the zygotes all lie in the cells of the female filament. There are also species in which the filaments are of mixed sex, and in these the zygotes may be formed in both of the conjugating filaments ; further, the presence of two filaments is not necessary, for the gametes can pass between cells of different sex in the same filament by means of a lateral conjugation canal (Fig. 349 *B*). There are also genera in which the zygote is situated midway in the conjugation tube (*Mesocarpus*).

The Conjugatae are a distinctly limited group of Green Algae. characterised by their cell-structure and method of reproduction. The phylogenetic connections of this group are by no means clear, Connecting forms between them and the Flagellates, or more probably the lower Chlorophyceae, have become extinct (23).

CLASS VII

Characeae (Stoneworts) (1, 11, 48)

The Characeae or Charophyta grow in ponds and ditches and sometimes form veritable meadows a foot in height. They are characterised by their thallus being constructed of elongated internodes separated by the nodes, by the whorled branching (Fig. 351), and by the type of their sexual organs. The oogonia have spirally-wound investing filaments, and the filamentous antheridia are contained within hollow spherical structures (Fig. 353).

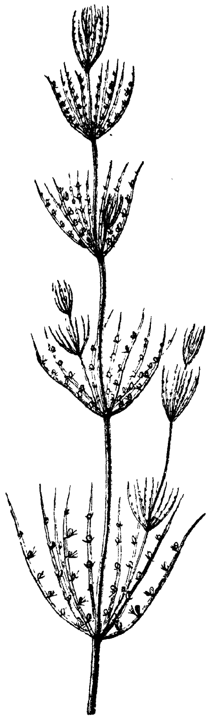


FIG. 351.—*Chara fragilis*. End of a main shoot. (Nat. size.)

The short shoots which arise in a whorl at each node are in their turn composed of nodes and internodes; they may be simple or bear at the nodes short branches of the second order.

From the axil of one of the short shoots of each whorl a lateral axis resembling the main axis is produced. The attachment to the substratum is effected by means of colourless branched rhizoids springing from the nodes at the base of the axes. The rhizoids show a similar segmentation into long internodal cells and nodal cells that are laterally displaced. Branching takes place at the nodes.

Both the main and lateral axes grow in length by means of an apical cell (Fig. 352), from which segments are successively cut off by the formation of transverse walls. Each of these segments is again divided by a transverse wall into two cells, from the lower of which a long internodal cell develops without further division; while the upper, by continued division, gives rise to a disc of nodal cells, the lateral axes, and also, in the lower portion of the main axis, to the rhizoids. In the genus *Nitella* the long internodes remain naked, but in the genus *Chara* they become enveloped by a cortical layer consisting of longitudinal rows of cells which develop at the nodes from the basal cells of the lateral axes.

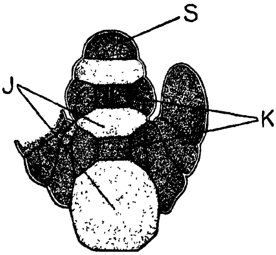
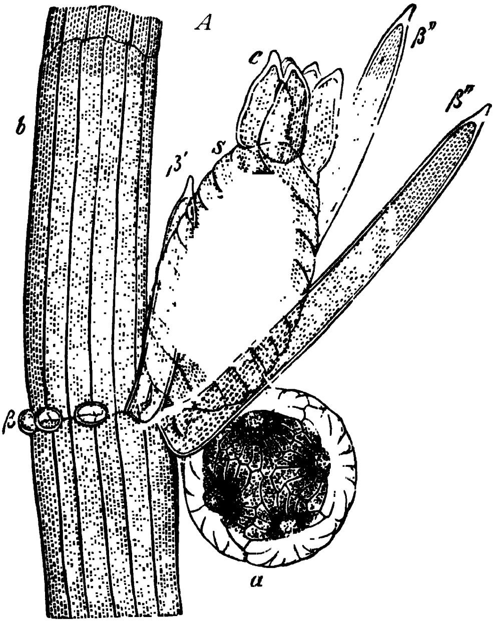


FIG. 352.—*Chara fragilis*. Longitudinal section of the apex; *S*, apical cell; *J*, internodes; *K*, nodes. (After SACHS, ×333.)

Each cell contains one normal nucleus derived from a karyokinetic division. As a result of the fragmentation of its original nucleus, however, each internodal cell is provided with a number of nuclei which lie embedded in an inner and actively-moving layer of parietal protoplasm. Numerous round GREEN CHLOROPLASTS are found in the internodal cells.

ASEXUAL REPRODUCTION by means of swarm-spores or other spores is wanting in the Characeae. SEXUAL REPRODUCTION, on the other hand, is provided for, by the production of egg-cells and spermatozoids. The FEMALE ORGANS or oogonia are ovate. They are visible to the naked eye, and, like the spherical red-coloured male organs, are inserted on the nodes of the lateral axes. With the exception of a few dioecious species, the Characeae are monoecious. The fertilised egg-cell develops into an oospore.



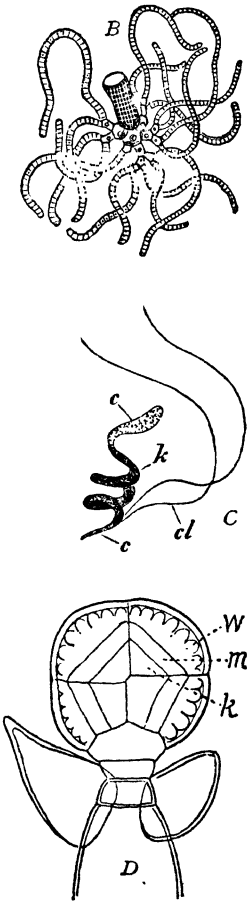


FIG. 353.—*A*, *Chara fragilis.* Lateral axis with the antheridial structure (*a*) and the oogonium (*s*) with its enveloping filaments and corona (*c*). *B*, *Nitella flexilis.* Manubrium with head-cells and spermatogenous filaments. *C*, *Chara fragilis.* Spermatozoid. *k*, nucleus; *cl*, cilia; *c*, cytoplasm (×540). *D*, *Nitella flexilis.* Longitudinal section through a young antheridial structure; *k*, head cells; *m*, manubrium; *w*, wall-cells. (*A*, *B*, *D*, after SACHS from OLTMANNS. *C*, after STRASBURGER.)

The MALE ORGANS (Fig. 353) are developed from a mother-cell that first becomes divided into eight cells. Each octant by two tangential walls gives rise to three cells. In this way are derived the eight external tabular cells of the wall, the cavities of which are incompletely partitioned by septa extending in from the cell-wall; the eight middle-cells form the manubria and become elongated; the eight innermost cells assume a spherical form as the primary head cells. Owing to the rapid surface growth of the eight shield-cells a cavity is formed within the male organ into which the manubria bearing the head-cells project. The latter form 3-6 secondary head-cells, and from each of these arise 3-5 long unbranched spermatogenous filaments (Fig. 353 *B*). These are composed of disc-shaped cells from each of which a spirally-wound spermatozoid with two cilia is liberated (Fig. 353 *C*). (The SPERMATOGENOUS FILAMENTS or antheridia may be compared morphologically to the plurilocular gametangia of the Brown Algae. These may consist of simple rows of cells and be grouped together in sori.)

The FEMALE ORGAN (Fig. 353 *A*, *s*) consists of an OOGONIUM which contains a single egg-cell with numerous oil-drops and starch grains. To begin with, the oogonium projects freely, but later becomes surrounded by five spirally-wound cells. These cells end in the corona, between the cells of which the spermatozoids make their way in fertilisation.

The egg, after fertilisation, now converted into an oospore, becomes invested with a thick colourless wall. The inner walls of the tubes become thickened and encrusted with a deposit of calcium carbonate, while the external walls of the tubes, soon after the fruit has been shed, become disintegrated.

In the germination of the oospore the nucleus divides into four, the first division being heterotypic. Thus the diploid stage is limited to the oospore, the Characeous plant itself being haploid. While three nuclei remain in the ventral portion of the zygote and there degenerate, the fourth nucleus enlarges and passes into the projecting germ-plant.

The formation of tuber-like bodies (bulbils, starch-stars) on the lower part of the axes is characteristic of some species of the Characeae. These tubers, which are densely filled with starch and serve as HIBERNATING ORGANS of vegetative reproduction, are either modified nodes with much-shortened branch whorls (*e.g.* in *Tolypellopsis stelligera*, where they are star-shaped), or correspond to modified rhizoids (*e.g.* the spherical white bulbils of *Chara aspera*).

FOSSIL CHARACEAE in the form of zygotes are known with certainty from the Jurassic. It is possible that certain Silurian fossils should also be placed here.

The Characeae form a phylogenetically isolated group of highly developed green Thallophytes. The peculiar construction of the thallus and of their sexual organs prevents any direct derivation of them from oogamous Green Algae.

CLASS VIII

Phaeophyceae (Brown Algae) (1, 11, 39-47)

The Phaeophyceae (42) are Algae of a characteristic brown colour. The chlorophyll (much *a* and little *b*) in their chromatophores is masked by the presence of carotin, xanthophyll, and especially by FUCOXANTHIN, a brown pigment allied to xanthophyll.

So far as is known, starch is never formed as the product of assimilation but instead the polysaccharide, LAMINARIN, which also serves as a reserve material, there are further mannite and oil, and, as a bye-product, a tannin-like substance FUCOSAN. Cellulose and pectic substances have been demonstrated in the cell-walls. The cells are uninucleate.

The motile stages (zoospores and gametes) without exception have two cilia inserted laterally on the pear- or spindle-shaped cell, in such a way that one cilium is directed forwards and the other backwards during movement (Fig. 354). In the neighbourhood of the cilia is a reddish-brown eye-spot and in the broader hinder end of the swarm-spore one, or less commonly several, brown chromatophores are situated.

With the exception of a few species that occur in fresh water the Phaeophyceae are marine algae and attain their highest development in the colder seas. The thallus exhibits a remarkable variety in form.

Order 1. Phaeosporales (43)

In this order are included the majority of the Brown Algae. One of the most widely distributed species is *Ectocarpus siliculosus*, the highly branched thallus of which, in its tufted form and delicate filaments, recalls the habit of the Green Alga, *Cladophora* (cf. Fig. 341). *Ectocarpus* is asexually reproduced by means of ZOOSPORES, which are formed in large numbers in UNILOCULAR SPORANGIA (Fig. 354) and germinate soon after they emerge. In sexual reproduction, multicellular GAMETANGIA are produced (plurilocular in contrast to the unilocular sporangia); from each of the small cells a single motile gamete develops (Fig. 355). These, though morphologically alike, exhibit in typical cases a sexual differentiation in their behaviour. The FEMALE GAMETE becomes attached to a substratum, and numerous MALE GAMETES gather around it (Fig. 356, 1). Ultimately a male gamete fuses with the female to form a zygote (Fig. 356, 2-9). This contains after the fusion a single nucleus but two chromatophores, and soon becomes attached and surrounded by a cell-wall; it grows into a new plant without undergoing a resting stage.

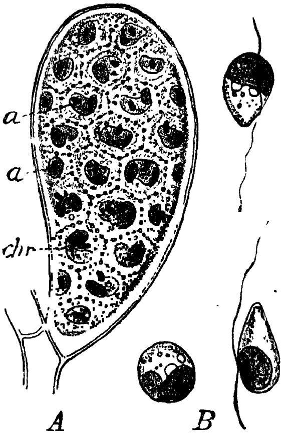


FIG. 354.—*A*, *Pleurocladia lacustris*. Unilocular sporangium with its contents divided up into the zoospores; *a*, eye-spot; *chr*, chromatophore. (After KLEBAHN.) *B*, *Chorda filum*. Zoospores. (After REINKE.) (From OLTMANNS' *Algae*.)

The sexual character of the gametes is not always well marked; on the one hand, they may develop parthenogenetically, and, on the other hand, fusion between gametes of the same sex may occur. Thus female gametes with ill-marked female tendencies can behave as male gametes towards well-marked female cells and conjugate with them (relative sexuality. HARTMANN) (44).

In other Phaeophyceae the distinction between the two kinds of gametes is sharper and is expressed in their shape and size. The Cutleriaceae afford a particularly good example, for the female gametangia are larger than the male (Fig. 357), and the plants are dioecious.

The REDUCTION-DIVISION occurs in the formation of the zoospores in the unilocular zoosporangia. The plants which bore these were diploid, while the zoospores give rise to haploid plants. These bear gametes, on the conjugation of which the diploid stage is again produced. There is thus a regular ALTERNATION OF GENERATIONS between an asexually reproducing generation or sporophyte and a gametophyte, which reproduces sexually. The two generations are further distinguished by their chromosome-numbers, the sporophyte being diploid and the gametophyte haploid. In some genera (*Pylaiella*, *Zanardinia*), the two generations are externally alike. In *Cutleria* (Fig. 365), on the other hand, they are dissimilar, the gametophyte being an erect dichotomous plant with fimbriate ends to its branches, while the sporophyte has the form of a flat, lobed, prostrate disc (*Aglaozonia*). The alternation of generations in the Phaeophyceae is not always strictly maintained and complications occur.

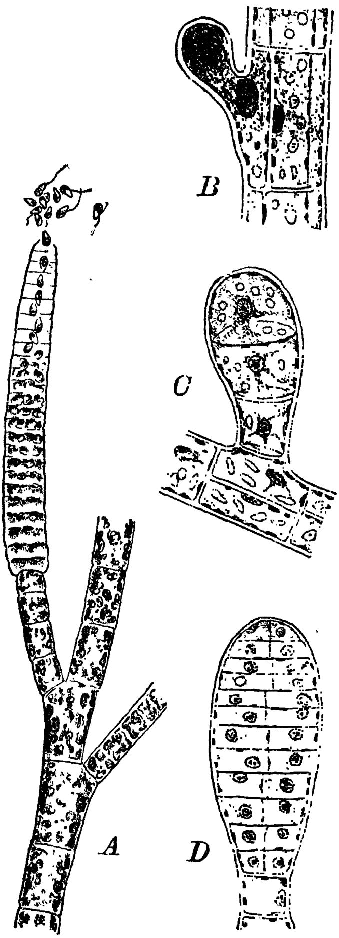


FIG. 355.—*A*, *Ectocarpus siliculosus*. Gametangium liberating its contents. (After THURET.) *B*, *C*, *D*, *Sphacelaria cirrhosa*, development of the gametangium. (After REINKE.) (From OLTMANNS' *Algae*.)

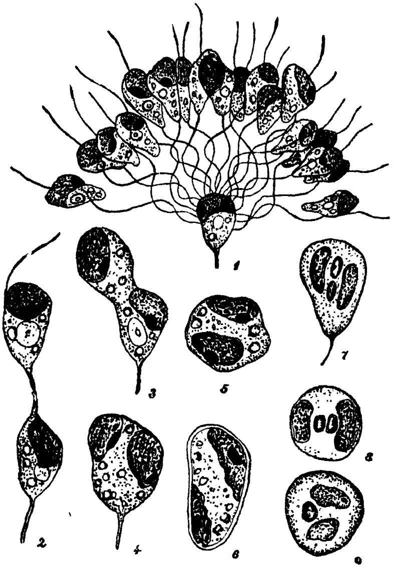


FIG. 356.—*Ectocarpus siliculosus*. *1*, Female gamete surrounded by a number of male gametes; seen from the side. *2-5*, Stages in the fusion of gametes. *6*, Zygote after 24 hours. *7-9*, Fusion of the nuclei in conjugation, as seen in fixed and stained material. (*1-5* after BERTHOLD; *6-9* after OLTMANNS.)

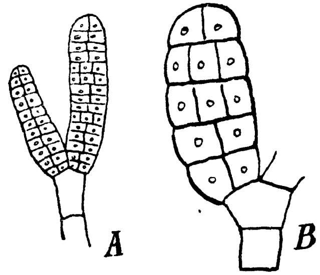
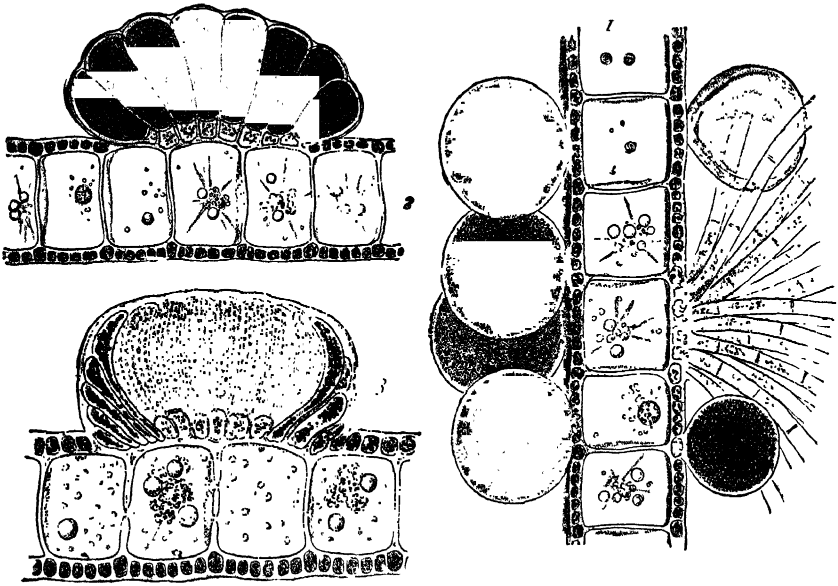


FIG. 357.—*A*, Two male gametangia; *B*, female gametangium of *Cutleria multifida*. (× 400. After REINKE.)

Order 2. Dictyotales (^{45}).

The Dictyotales are more highly developed than the Phaeosporales in two respects; their vegetative body is of more complex structure and their sexual reproduction is typically oogamous.

Dictyota dichotoma, which is widely distributed on the European coast, has a ribbon-shaped, dichotomously branched thallus (Fig. 80). The sporophyte and gametophyte, which form parts of a regular ALTERNATION OF GENERATIONS, are exactly alike in form and structure. The asexual generation which develops from the diploid zygote forms shortly stalked, spherical, unilocular TETRASPORANGIA on the surface of the thallus (Fig. 358, 1). Within these, following a reduction-division, four naked spores (TETRASPORES) are developed; in contrast to the other Brown Algae these are without cilia and non-motile. They are transported passively by the water and germinate to form haploid plants, which are either male or female. On the male plants groups (sori) of plurilocular ANTHERIDIA (Fig. 358, 3) are developed; from each of the cells of these a pear-shaped spermatozoid with a single laterally-placed cilium (Fig. 358, 4) is produced. Groups of OOGONIA (Fig. 358, 2) are borne on the female plants; the oogonia are unicellular and each produces a single, large, non-motile egg-cell. After fertilisation this develops into a sporophyte without undergoing any period of rest.



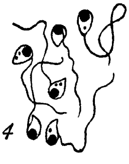


FIG. 358.—*Dictyota dichotoma.* Transverse sections of the thallus. *1*, With tetrasporangia; *2*, with a group of oogonia; *3*, with a group of antheridia (after THURET). *4*, Spermatozoids (after WILLIAMS). (From OLTMANNS *Algae*.)

Order 3. Laminariales (^{46})

In the alternation of generations of the oogamous Laminariales the sexual generation is very small, while the sporophyte is large and in many genera attains a great size (Fig. 359). From the haploid zoospores, minute filamentous male and female GAMETOPHYTES develop (Fig. 360). The former are abundantly branched, while the latter consist of few cells and in extreme cases may be reduced to a single cell. The male gametophytes bear the antheridia at the tips of the branches. Each antheridium gives rise to one biciliate spermatozoid. Any cell of the female gametophyte may form an oogonium, from an opening at the summit of which the naked egg-cell emerges. This remains in front of the opening, and after fertilisation, proceeds to grow into the diploid SPOROPHYTE. This bears club-shaped or cylindrical sporangia forming an extensive superficial layer. Each surface cell of the thallus is prolonged as a club-shaped sterile cell or paraphysis, beside which the sporangia arise as shorter cells. The reduction-division takes place in the sporangia, and numerous biciliate zoospores are produced.

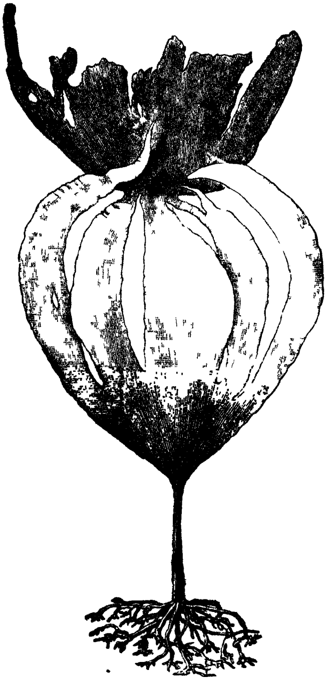


FIG. 359.—*Laminaria Cloustoni*, North Sea. Sporophyte as it occurs in April. (Reduced to ⅛.)

The sporophytes in the Laminariales are frequently of large size and exhibit a high degree of morphological and anatomical differentiation. Thus *Macrocystis pyrifera* (39) (Fig. 361) attains a length of 70 metres in the Antarctic; the thallus grows firmly attached to the sea-bottom at a depth of 2-25 metres. The axis bears along one side long pendulous thalloid lobes, at the base of each of which is a large air-bladder, by means of which the plant is kept floating along the surface of the sea (Fig. 361). Other noteworthy forms are the Antarctic species of *Lessonia*, in which the main axis is as thick as a man's thigh; from it are given off lateral branches with pendulous leaf-like segments. The plant attains a height of several metres, and has a tree-like habit of growth. The species of *Laminaria* in the North Sea (Fig. 359) are several metres in length. Some of them bear, on the end of a perennial stalk of the thickness of the thumb, a simple or palmately divided leaf-like expansion of the thallus. This is renewed annually, since, towards the end of the winter, an intercalary zone at the base of the blade gives rise to a new expanded region; the old blade is pushed up by this and gradually perishes

Order 4. Fucales (47)

Asexual reproduction is wanting in this order, while sexual reproduction is distinctly oogamous.

The species of *Fucus* have ribbon-shaped, dichotomously branched thalli which may be over a metre in length. The thallus is firm and leathery and attached to the rock by a discoid holdfast (Fig. 362). *Fucus* covers extended areas of the littoral region of the coasts of Northern Europe. *Fucus serratus* has the thallus toothed, while *F. vesiculosus* has air-bladders in the thallus. The highest differentiation is attained by the thallus of *Sargassum* (41); this shows a distinction of cylindrical axes and lateral branches, which, according to their functions, are developed as foliage, bracteal or fertile branches, or as air-bladders. *Sargassum* grows on the coasts of the West Indies and tropical America, but is carried in large quantity in the detached condition by currents to the region of the Atlantic Ocean called the Sargasso Sea, where it leads a pelagic existence.

The oogonia and antheridia of *Fucus* are formed in special flask-shaped depressions termed CONCEPTACLES, which are crowded together below the surface in the swollen tips of the dichotomously-branched thallus (cf. *F. serratus*, Fig. 362). The conceptacles of *F. platycarpus* (Fig. 363) contain both oogonia and antheridia, while *F. vesiculosus* and *F. serratus* on the contrary are dioecious.

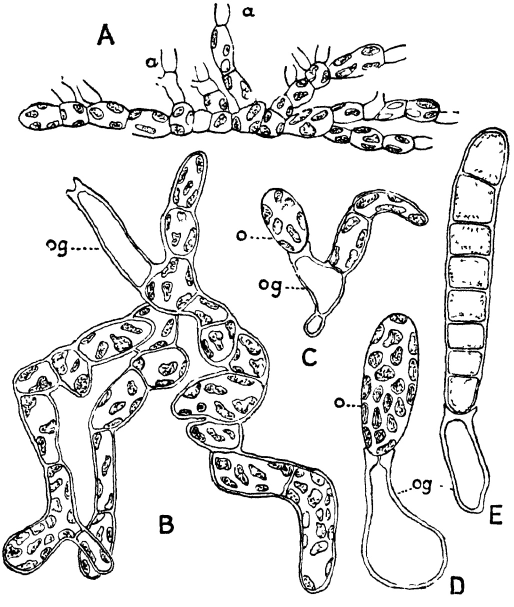


FIG. 360.—*Laminaria digitata.* *A*, Male gametophyte; *a*, empty antheridia. *B*, *C*, *D*, Female gametophytes (*B* is large, *C* small, while *D* is reduced to a single oogonium); *og*, oogonium; *o*, egg-cell. *E*, Young sporophyte, still seated on the empty oogonium. (*A* × 600; *B* × 292; *C* × 322; *D* × 625; *E* × 322. After H. KYLIN.)

From the inner wall of the conceptacles spring numerous unbranched sterile hairs or PARAPHYSES, some of which protrude in tufts from the mouth of the conceptacle (Fig. 363 *p*). The ANTHERIDIA are oval in shape, and are formed in clusters on special short and much-branched filaments (Figs. 363 *a*, 364, 1). The contents of each antheridium separate into sixty-four spermatozoids, which are discharged in a mass, still enclosed within the inner layer of the antheridial wall (Fig. 364, 2). Eventually set free from this outer covering, the spermatozoids appear as somewhat elongated ovate bodies, having two lateral cilia of unequal length and a red eye-spot. The OOGONIA (Figs. 363 *o*; 364, 3) are nearly spherical, and are borne on short stalks consisting of a single cell. They are of a yellowish-brown colour, and enclose eight spherical egg-cells, which are formed by the division of the oogonium mother-cell. The eggs are enclosed within a thin membrane when ejected from the oogonium. This membranous envelope deliquesces at one end and, turning partly inside out, sets free the eggs (Fig. 364, 4, 5). The spermatozoids then gather round the eggs in such numbers that by the energy of their movements they often set them in rotation (Fig. 364, 6). After an egg has been fertilised by the entrance of one of the spermatozoids it becomes invested with a cell-wall, attaches itself to the substratum, and gives rise by division to a new plant.

In the case of other Fucaceae, which produce four, two, or even only one egg in their oogonia, the nucleus of each oogonium, according to OLTMANNS, nevertheless first divides into eight daughter-nuclei; of these, however, only the proper number give rise to eggs capable of undergoing fertilisation. The other eggs, incapable of fertilisation, degenerate. In this division the reduction in number of the chromosomes takes place; the plant of *Fucus* is diploid.

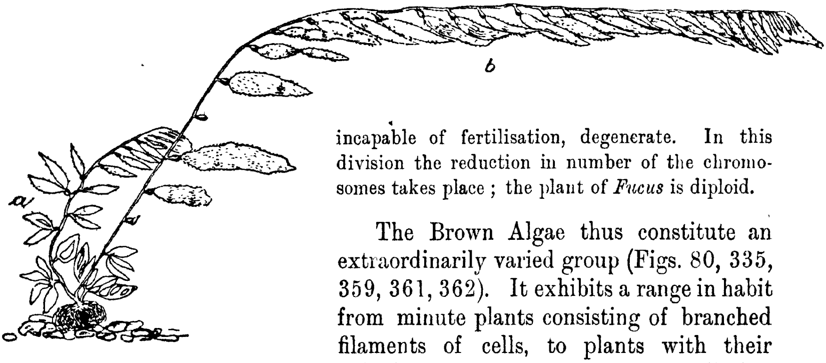


FIG. 361.—*Macrocystis pyrifera*, Ag. *a*, Younger, *b*, older thallus. ($\frac{1}{80}$ nat. size. After SKOTTSBERG.)

The Brown Algae thus constitute an extraordinarily varied group (Figs. 80, 335, 359, 361, 362). It exhibits a range in habit from minute plants consisting of branched filaments of cells, to plants with their cells forming a massive tissue, exhibiting an external differentiation that suggests comparison with leaves, stem, and roots, and attaining a height of many decimetres, or even that of a small tree.

They are always attached, often by means of special discoid holdfasts or branched root-like organs of attachment. The larger forms grow on rocks, while some of the smaller forms are epiphytic.

The anatomical structure corresponds to the highly differentiated external form. The thallus often grows by means of a large apical cell (Fig. 86, 87). There is usually a distinction between external assimilating tissues and internal storage cells (Fig. 358). In some cases (Laminariales and Fucales) there are tubular structures, which are constructed like the sieve-tubes of the Cormophytes and serve similarly for the conduction of albuminous substances.

The Phaeophyceae constitute a parallel phylum to the Chlorophyceae.

They appear, like the latter, to have originated from the Flagellatae, and this is borne out by the resemblance of their swarm-spores to Flagellates. It is not possible, however, to establish a direct connection between them and the brown Flagellates, since intermediate forms are wanting; even the lowest Phaeophyceae are relatively advanced forms with sporangia and gametangia. There is also no close relationship with the filamentous Chrysophyceae, partly because these can form swarm-spores from any cell, and also because the motile-cells differ in their construction.

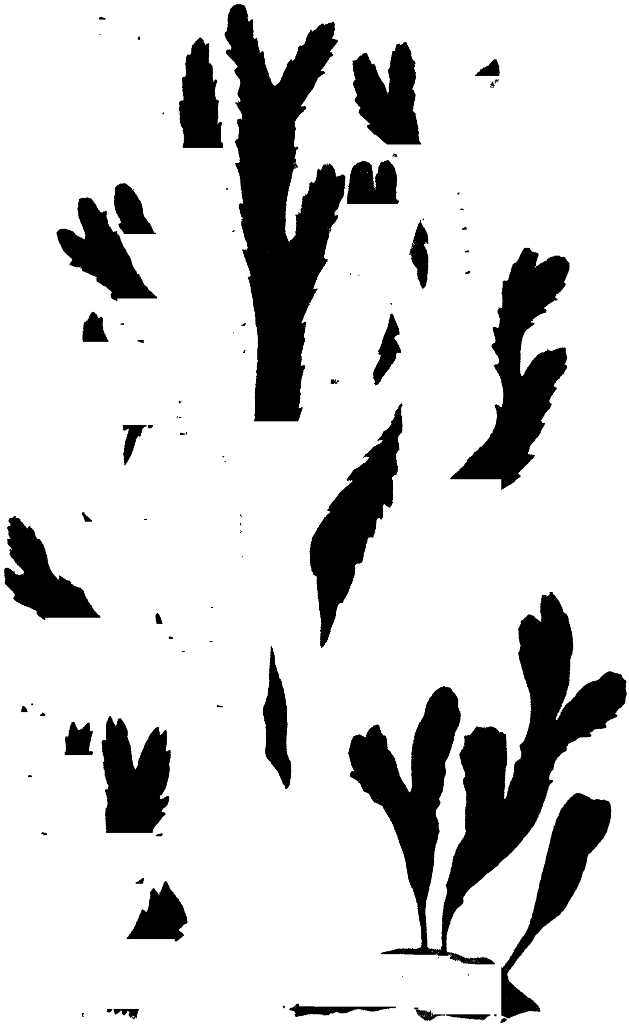


Fig. 362.—*Fucus serratus*. To the left the end of an older branch bearing conceptacles. (⅓ nat. size.)

As in the Chlorophyceae, a passage from isogamy to oogamy can be followed in the Brown Algae. In the lower forms (*Ectocarpus*) the gametangia of the two sexes are alike and multicellular; in higher forms (*Cutleria*) the female gametes are larger than the male, while in *Dictyota* only a single egg is formed in the oogonium. In *Dictyota* the antheridia are still multicellular, but in *Laminaria* they also have become unicellular and only form a single spermatozoid. Plurilocular gametangia, antheridia, and oogonia are thus homologous structures.

In contrast to the Chlorophyceae the Phaeophyceae mostly have a regular alternation of generations, which is, however, rather ill-defined in the primitive Phaeosporales, and only appears with complete distinctness in the higher groups. The construction of the sporophyte and gametophyte may be the same (*Pylaiella*, *Dictyota*), or the generations may differ markedly in habit (*Cutleria*, *Laminaria*). Either the gametophyte (*Cutleria*) or the sporophyte (*Laminaria*) may be the more strongly developed generation (Fig. 365). The sporophyte is always diploid, and the gametophyte haploid, since the reduction-division takes place at the formation of the asexual spores.

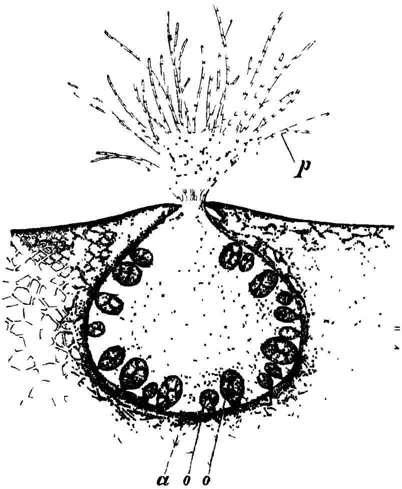


FIG. 363. — *Fucus platycarpus*. Monoecious conceptacle with oogonia of different ages (o), and clusters of antheridia (a), p, paraphyses. (× circa 25 After THURET)

The Fucales occupy an isolated position, since no alternation of generations is evident in them. It has been seen, however, how in the Laminariales, the female gametophyte sometimes consists of only one cell and the contents of the zoospore after coming to rest thus become the egg-cell (Fig. 360, *D*). The behaviour of *Fucus* may therefore be accounted for by supposing that the reduction of the gametophyte has gone a stage further and the asexual spore has itself become the egg-cell. The Fucales are thus the terminal member in a series exhibiting a progressive reduction of the gametophyte.

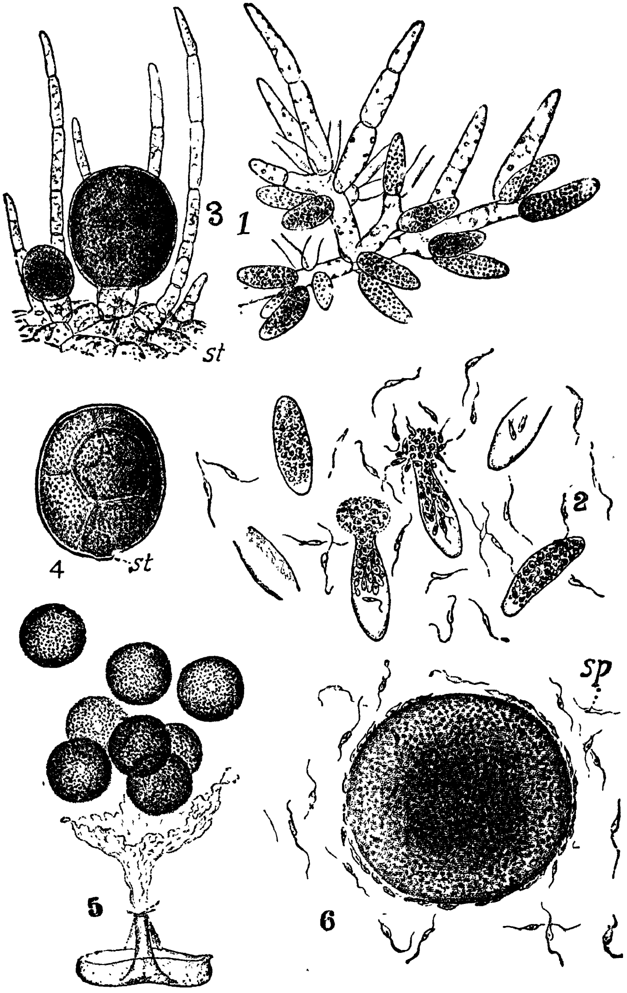


FIG. 364.—*Fucus*. *1*, Group of antheridia. *2*, Antheridia showing escaping spermatozoids. *3*, Oogonium, the contents of which have divided into eight egg-cells. *4*, Contents separated from stalk (*st*). *5*, Liberation of the egg-cells. *6*, Oosphere surrounded by spermatozoids. (After THURET. From OLTMANNS' *Algae*).

In addition to differences in habit, the following characters serve to distinguish the Orders:

Phaeosporales. Asexual reproduction by zoospores; sexual reproduction by ciliated iso- or hetero-gametes. In some an alternation of generations.

Dictyotales. Asexual reproduction by non-motile tetraspores; sexual reproduction oogamous. Alternation of generations; sporophyte and gametophyte alike.

Laminariales. Asexual reproduction by zoospores; sexual reproduction oogamous. Alternation of generations; gametophyte minute.

Fucales. Reproduction only by oogamy.

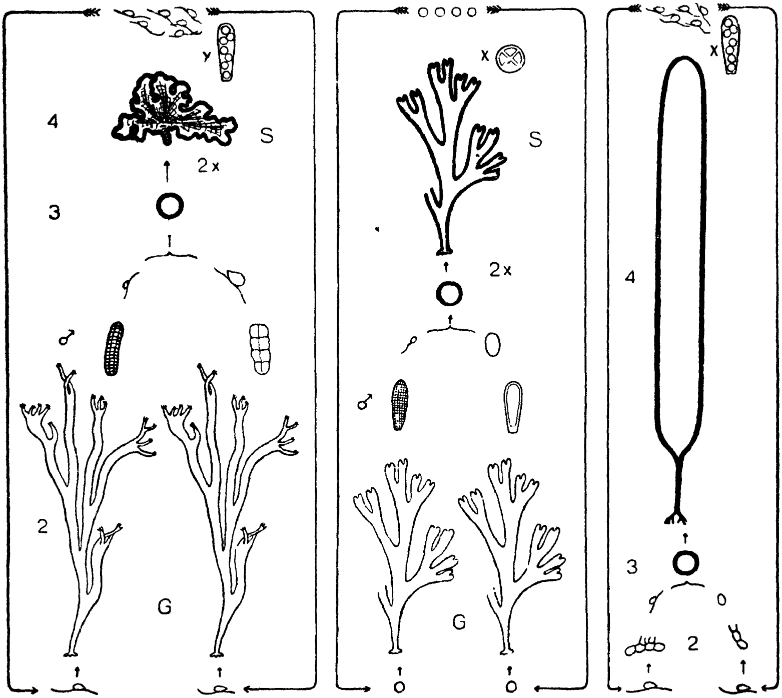


FIG. 365.—Diagrammatic representation of the alternation of generations and of phases in *Cutleria* (left), *Dictyota* (centre), and *Laminaria* (right). *G*, gametophyte; *S*, sporophyte; *x*, haploid (thin lines); 2 *x*, diploid (thick lines).

Economic Uses.—The dried stalks of *Laminaria digitata* and *L. Cloustoni* were formerly used as dilating agents in surgery. IODINE is obtained from the ash (varec, kelp) of various Laminariaceae and Fucaceae, and formerly soda was similarly obtained. Many Laminarias are rich in MANNITE (*e g. Laminaria saccharina*), and are used in its production, and also as an article of food by the Chinese and Japanese.

CLASS IX

Rhodophyceae (Red Algae) (1, 11, 28, 49, 50)

The Rhodophyceae or Florideae are usually red or violet; sometimes, however, they have a dark purple or reddish-brown colour. Their chromatophores, which are flat, discoid, oval, or irregular-shaped bodies, contain a red pigment, PHYCOERYTHRIN, and in some cases a blue pigment (PHYCOCYAN) in addition.

True starch is never formed as a product of assimilation, its place being taken by other substances, very frequently, for example, by Floridean starch, in the form of spherical stratified grains which stain red with iodine; this is more closely allied to glycogen than to starch. Oil-drops also occur. Practically all the Rhodophyceae are autotrophic, but a few species are without chromatophores and live as parasites on other Algae. An example is *Harveyella mirabilis* (^{50}), which occurs as small cushion-like growths on *Rhodomela subfusca* in the North Sea.

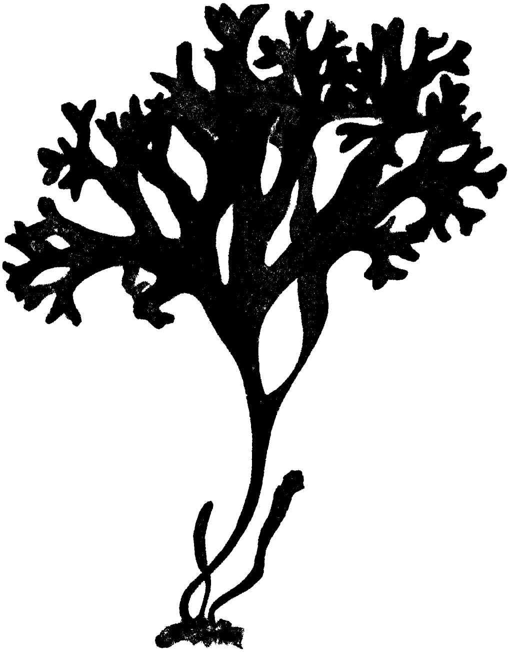


FIG. 366.—*Chondrus crispus*. (½ nat. size.)

With few exceptions (*e.g. Batrachospermum*) the Rhodophyceae are marine. They are attached by special growths of filaments or by discoid holdfasts. The thallus of the Red Algae exhibits a great variety of forms.

The simplest forms are represented by branched filaments consisting of single rows of cells (*e.g. Callithamnion*). In many forms the thallus is flattened and ribbon-like (*e.g. Chondrus crispus*, Fig. 366; *Gigartina mamillosa*, Fig. 367); while in other species it consists of expanded cell-surfaces, attached to a substratum. One of the more complicated forms is *Delesseria* (*Hydrolapathum*) *sanguinea* (Fig. 85), which occurs on the coasts of the Atlantic. The leaf-like thallus, which springs from an attaching disc, is provided with mid-ribs and lateral ribs. In the autumn the wing-like expansions of the thallus are lost, but the main ribs persist and give rise to new leaf-like branches in the succeeding spring. The thalli of the Corallinaceae, which have the form of branch-systems or of flattened or tuberculate incrustations, are especially characterised by their coral-like appearance, owing to the large amount of calcium carbonate deposited in their cell-walls. The calcareous Florideae are chiefly found on coasts exposed to a strong surf, especially in the tropics.

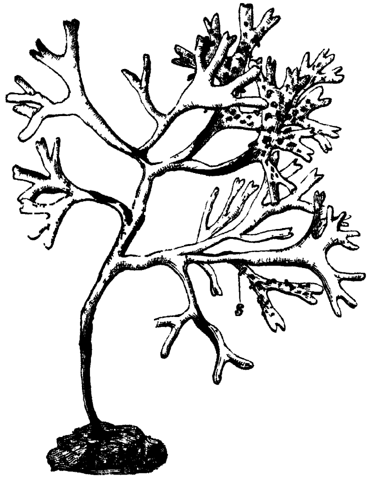


FIG. 367.—*Gigartina mamillosa.* *s*, Wart-shaped cystocarps. ($\frac{2}{3}$ nat. size.)

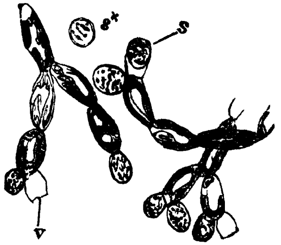


FIG. 368.—*Batrachospermum moniliforme.* Branches bearing antheridia. At *s**, a free spermatium; at *s*, another just escaping; at *v*, an empty antheridium. (× 540. After STRASBURGER.)

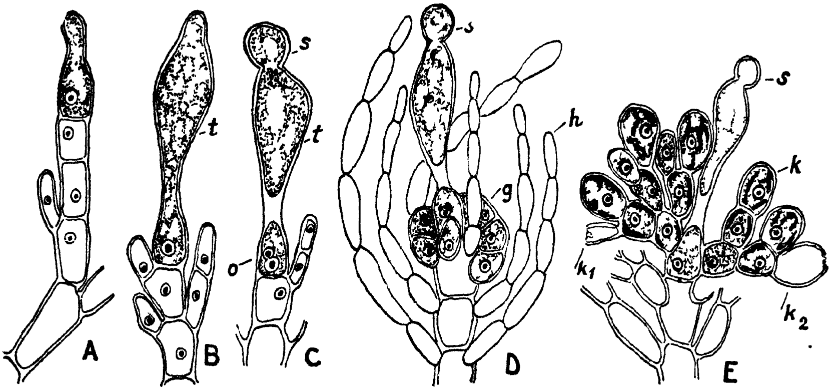


FIG. 369.—*Batrachospermum moniliforme.* *A*, Young carpogonium terminating a branch. *B*, Ripe carpogonium; *t*, trichogyne. *C*, Stage after fertilisation by the spermatium (*s*), the egg-cell (*o*) containing the two sexual nuclei. *D*, Sporogenous filaments (*g*) and investing filaments (*h*). *E*, Some of the mature sporogenous filaments with the carpospores (*k*); these have emerged from k_1 and k_2. (*A*-*D* × 960, *E* × 720. After H. KYLIN.)

It is characteristic of all Rhodophyceae that THEIR REPRODUCTIVE CELLS, WHETHER ASEXUAL SPORES OR GAMETES, ARE NON-MOTILE.

The sexual reproduction is OOGAMOUS, the female gametangium, which is termed a CARPOGONIUM, having a long, slender receptive organ, the TRICHOGYNE (Fig. 369). On fertilisation the zygote germinates at once in a characteristic fashion without leaving the carpogonium; it develops SPOROGENOUS FILAMENTS which produce the asexual spores.

There is extraordinary variety in the details of the reproduction. Without attempting a description of the various orders some characteristic examples may be described.

Batrachospermum moniliforme, which occurs attached to stones in mountain streams, has a brownish or dark violet thallus enveloped in mucilage and consists of verticillately branched filaments (Fig. 372) The ANTHERIDIA (Fig. 368) are produced, usually in pairs, at the ends of the radiating branches. Each antheridium consists of one cell, the protoplast of which produces a single spherical, colourless, naked, male gamete. Since it has no cilia it is not termed a spermatozoid but a SPERMATIUM. The female CARPOGONIA are similarly placed at the ends of branches near the antheridia. They consist of an elongated cell with a basal flask-shaped portion and a club-shaped upper continuation; this upper region, which in most Red Algae is elongated and slender, is termed the TRICHOGYNE. The nucleus of the egg is situated in the basal swollen region. The non-motile spermatium is carried passively by the movement of the water to the trichogyne, to which it adheres; it then surrounds itself with a cell-wall, and its contents pass through an opening into the carpogonium.

After the fusion of the male and female nuclei the basal portion of the carpogonium enclosing the fusion-nucleus becomes separated by a wall from the trichogyne. No oospore is formed, but from the sides of the basal portion of the carpogonium branched filaments of cells, the sporogenous filaments, grow out. At the same time, by the development of outgrowths from the cells below the carpogonium, the sporogenous filaments are enclosed, the whole structure being termed a CYSTOCARP (Fig. 369 *D*). In the swollen ends of the sporogenous filaments spherical spores (CARPOSPORES), each with one nucleus and a chromatophore, are produced. They are extruded from the cells as spherical, naked, non-motile structures. The carpospores are asexual spores; they grow into a protonema-like structure, which may reproduce vegetatively by monospores, and upon this the shoots of the sexual *Batrachospermum* plant arise later.

There is thus a regular ALTERNATION OF GENERATIONS between the GAMETOPHYTE (*Batrachospermum* plant) and a CARPOSPOROPHYTE, consisting of the sporogenous filaments forming the carpospores. The sporophyte does not, however, constitute a distinct plant but remains attached to the gametophyte.

These relations cannot be regarded as strictly homologous with the alternation of generations of the Brown Algae, since the REDUCTION-DIVISION occurs in a different place. It takes place not at the formation of the carpospores but on the first division of the fertilised nucleus of the egg. The carposporophyte is therefore, like the gametophyte, haploid and the diplophase is restricted to the zygote (Fig. 372).

The relations that have been described for *Batrachospermum* hold also for the marine alga *Nemalion* and some other genera.

Dudresnaya coccinea, which is found on the warmer coasts of Europe, has a branched, cylindrical thallus and will serve as an example of the more complicated mode of origin of the spore-bearing generation (Fig. 370). The carpogonium which is borne on a short branch bears a very long trichogyne. After fertilisation the carpogonial cell grows out into filaments, which elongate and become branched; these fuse with a number of special cells, characterised by their abundant contents, the AUXILIARY CELLS. The successive fusions with auxiliary cells do not involve nuclear fusions, but simply serve to nourish the sporogenous filament. Two outgrowths now arise from each of the swollen cells of the sporogenous filament which fused with auxiliary cells. By further division of these outgrowths the spherical masses of carpospores, which subsequently become free, are derived.

The life-history in some other genera (*e g. Polysiphonia*, *Delesseria*, *Rhodomela*, etc.) is more complicated than in the examples so far considered. In them the carpospore does not give rise to a gametophyte but to a plant which, though it completely resembles the sexual plant in habit, does not bear sexual organs but reproduces by means of asexual spores; these are always borne in a TETRASPORANGIUM containing four TETRASPORES. It is these tetraspores which on germination give rise to a gametophyte, so that in these cases three generations succeed one another in the life-history: gametophyte, carposporophyte, tetrasporophyte. The reduction-division does not occur in the division of the nucleus of the zygote but in the tetrasporangium at the formation of the tetraspores. The two sporophyte generations are thus diploid (as in the Brown Algae), while the gametophyte is haploid (Fig. 372).

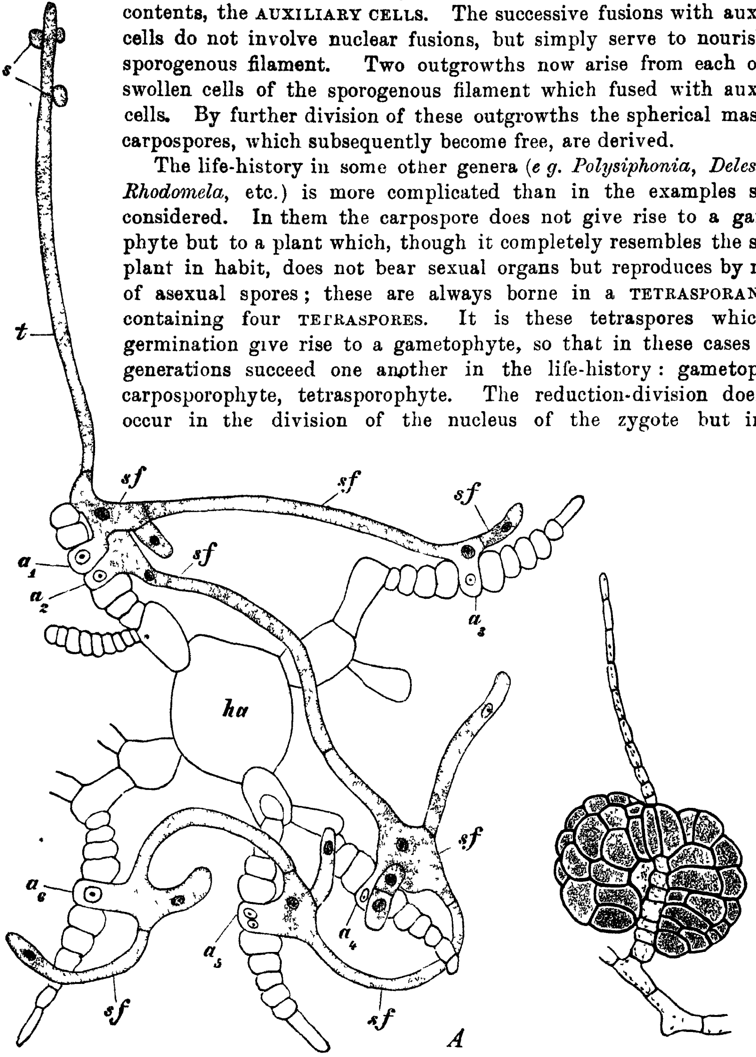


FIG. 370.—*Dudresnaya.* *A*, The fertilised carpogonium with spermatia (*s*) attached to the trichogyne (*t*) has grown out to sporogenous filaments; branching of the filament and fusion with six auxiliary cells (a_1-a_6); the cells a_3-a_6 are borne on branches originating from the axis *ha*. *B*, Ripe cluster of carpospores originating from one branch. (*A* after OLTMANNS; *B* after BORNET. × about 250.)

These examples do not give a complete idea of the variety in the reproductive processes in the Red Algae.

The phylogenetic position of the Rhodophyceae is still quite obscure. The majority of systematists incline to a derivation from the Chlorophyceae by way of *Coleochaete.*

Red Algae (Corallinaceae) are known with certainty from the Cretaceous period ; from earlier formations, back to the Ordovician, impressions of non-calcified, *Delesseria*-like forms are known.

Economic Uses.—*Gigartina mamillosa* (Fig. 365), with peg-like cystocarps 2·5 mm. in length, and *Chondrus crispus* (Fig. 364), with oval cystocarps about 2 mm. long, sunk in the thallus and tetraspores in groups on the terminal segments of the thallus. Both forms occur in the North Sea as purplish-red or purplish-brown Algae ; when dried they have a light yellow colour, and furnish the official CARRAGHEEN, "Irish Moss," used in the preparation of jelly. AGAR-AGAR, which is used for a similar purpose, is obtained from various Florideae ; *Sphaerococcus* (*Gracilaria*) *lichenoides* supplies the Agar of Ceylon (also called Fucus amylaceus), *Eucheuma spinosum* the Agar of Java and Macassar, and species of *Gelidium*, the Agar of Japan.

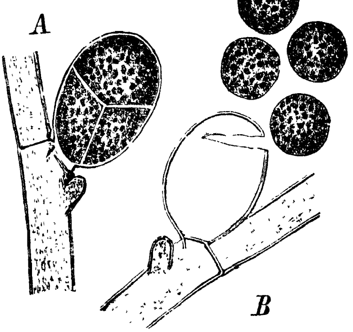


FIG. 371.—*Callithamnion corymbosum. A*, Closed sporangium ; *B*, empty sporangium with four extruded tetraspores. (After THURET.)

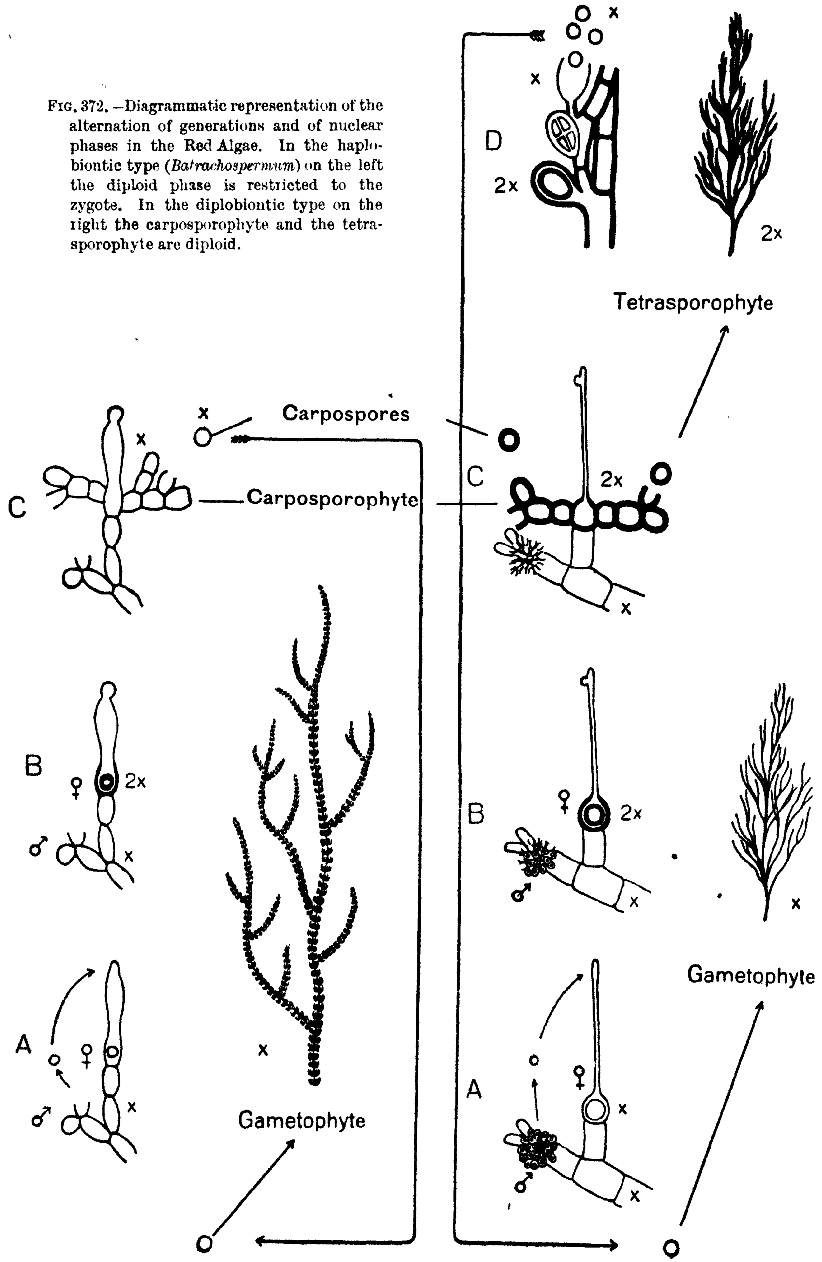
Survey of the Algae

The Algae are a group of organisms which connect on to the Flagellatae by their simplest forms and have developed polyphyletically in several main series to highly differentiated plants (Fig. 531). The case for the connection of the Green Algae with the Flagellates is clear ; only the Charales are isolated from the rest of the group. In the Brown Algae, where unicellular forms are wanting, the connection with the Flagellatae is somewhat less certain, and, on our present knowledge, the Red Algae still occupy an isolated position.

The Red Algae and especially the Brown Algae attain a higher organisation of the thallus than do the Green Algae. They are further more highly organised in having a regular alternation of generations which is still lacking in the Green Algae.

Only a relatively small number of simply organised algae lead a terrestrial life, though a number of littoral marine forms are exposed to the air at low tide. The remaining algae, including the majority of those that are most highly differentiated, are completely submerged ; this is evidently connected with the absence of special tissues for the conduction of water in the plant. They occur in fresh water and in the sea. While some kinds (*e.g Ulva*) can establish themselves in brackish water, most marine forms become dwarfed when the water is less salt, and ultimately, as the freshness of the water increases, disappear. Thus in the western portion of the Baltic, *Laminaria* still occurs in the form of dwarf plants while it is wanting altogether in the eastern portion. *Fucus* on the other hand

Fig. 372.—Diagrammatic representation of the alternation of generations and of nuclear phases in the Red Algae. In the haplobiontic type (*Batrachospermum*) on the left the diploid phase is restricted to the zygote. In the diplobiontic type on the right the carposporophyte and the tetrasporophyte are diploid.



grows luxuriantly in the former region, and still occurs in the region where *Laminaria* is unable to exist, but only in the form of dwarf plants which do not bear reproductive organs.

A stratified arrangement is evident in the occurrence of the various groups of Algae when the water is of considerable depth. The Green Algae almost without exception occupy positions near the surface, they are succeeded by the Brown Algae, while the Red Algae inhabit the deepest zone down to 120 metres. This distribution agrees with the theory of ENGELMANN that water absorbs the red rays more strongly than the green and blue rays. Thus in the deeper parts the prevailing light is that of short wave-length, which is complementary to the colour of the Red Algae and can be utilised by them, but not by the Green Algae, in assimilation. At the same time the intensity of the illumination is weakened so that according to OLTMANNS the algae of the deeper regions are shade-plants, which can assimilate in light of less intensity than that required by the forms growing near the surface. This explains why Red Algae occupy the more shaded positions in pools, clefts, etc. As in the case of every rule there are exceptions; some Red Algae, especially the Corallinaceae of tropical seas but also some forms in our own seas, inhabit situations exposed to direct sunlight.

Some of the lower Chlorophyceae can be artificially grown in pure culture and can even be cultivated on solid substrata. The cultivation of Brown and Red Algae is still a matter of great difficulty. Among the lower forms some can utilise organic food materials to a certain extent.

CLASS X

Myxomycetes (Slime Fungi) (1, 13, 14, 15)

The Myxomycetes, which have no chlorophyll, lead again to the consideration of primitive, phylogenetically ancient organisms. In the vegetative condition they consist of naked amoeboid masses of protoplasm, with animal nutrition; from these, following on a sexual process, enclosed sporangia containing asexual spores are developed.

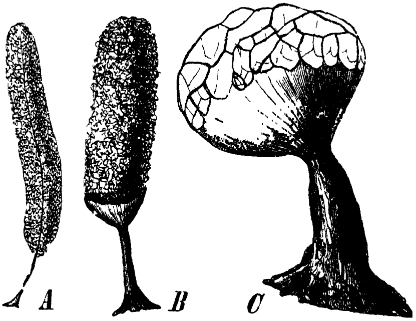


FIG. 373.—Ripe fructifications, after discharge of the spores. *A*, *Stemonitis fusca* (× 10); *B*, *Arcyria punicea* (× 12), *C*, *Cribraria rufa* (× 32).

The development of Myxomycetes proceeds in the following way. The germination of the spores (Fig. 375, *Chondrioderma*) takes place in water or on a wet substratum. The protoplast, on escaping from the spore, develops a flagellum or cilium as an organ of motion, being converted into a SWARM-SPORE which resembles certain Flagellata, with a cell-nucleus in its anterior or ciliated end, and a contractile vacuole in the posterior end of its body, but no chromatophores. The nutrition is saprophytic.

In some species the swarm-spores can increase in number by fission. Eventually the cilium is drawn in, and the swarm-spore becomes transformed into a MYXAMOEBA (Fig. 375); these have the capacity of multiplication by division (Fig. 376 *A*, *B*). In conditions unfavourable for their development they surround themselves with walls, and as MICROCYSTS pass into a state of rest, from which, under favourable conditions, they again emerge as swarm-spores.

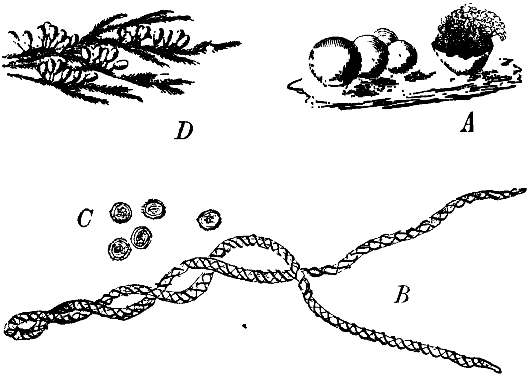


FIG. 374.—*Trichia varia*. *A*, Closed and open sporangia (× 6); *B*, a fibre of the capillitium (× 240); *C*, spores (× 240). *D*, *Leocarpus fragilis*. Groups of sporangia upon a Moss. (Nat. size.)

THE UNINUCLEATE MYXAMOEBAE FUSE [14] IN PAIRS, THEIR HAPLOID NUCLEI UNITING (Fig. 376, *C*). The diploid AMOEBOZYGOTES, which have in this way arisen by a sexual process, do not become resting spores but continue to exist as naked protoplasts. They unite in numbers to form larger multinucleate PLASMODIA (Fig. 4), the nuclei of which increase in number by repeated mitotic division.

The plasmodia can take up Bacteria and other solid nutritive particles and digest them in vacuoles (Fig. 376, *D*). As a reserve material they form glycogen, not starch. They occur especially on the soil of woods, on fallen leaves and in decaying wood, where they creep about exhibiting continual change of form. They reach situations favourable to their nutrition by means of their chemotactic, hydrotactic and negatively phototactic movements. The plasmodia of some species (*e.g. Fuligo varians*=*Aethalium septicum*, Flowers of Tan) may reach a diameter of over 30 cm. If exposed to desiccation some plasmodia pass into a resting state and become converted into spherical or strand-like SCLEROTIA, from which a plasmodium is again produced on a return of moist conditions.

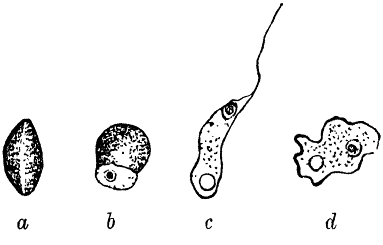


FIG. 375.—*Chondrioderma difforme*. *a*, Dry spore; *b*, spore showing escaping contents; *c*, swarm-spore; *d*, myxamoeba. Cf. Fig. 4. (× 540. After STRASBURGER.)

The SPORANGIA are formed from the plasmodia. The plasmodium changes its irritability, creeping from the moist substratum and towards the light. It loses a considerable amount of water and is transformed into numerous FRUCTIFICATIONS. Each of these has a firm peripheral investment (PERIDIUM), which often contains lime, and numerous uninucleate SPORES. The spores have firm cell-walls that do not however consist, as is common in the Fungi, of chitin. The division immediately preceding spore-formation is a reduction-division, so that the spores are haploid.

In many genera a CAPILLITIUM is also present (Figs. 373 *A*, *B*, 374 *A*, *B*), which arises from coagulating protoplasm between the spores and has the form of fine tubes or threads that are either free or reticulately connected. When the fructification is ripe the peridium ruptures, the capillitium loosens out and expands, and the spores are distributed by means of its hygroscopic movements and the wind. The genus *Ceratiomyxa* is in a sense simpler, since its fructifications have no peridium but bear the spores on short pedicels projecting from the surface.

The structure and nature of the sporangia afford the most convenient means of distinguishing the different genera. The usually brown or yellow sporangia are spherical, oval, or cylindrical, stalked (Figs. 373, 374 *D*), or not stalked (Fig. 374 *A*). They usually open by the rupture of the upper portion of the sporangial walls, the lower portion persisting as a cup (Figs. 373 *B*, 374 *A*). In *Cribraria* (Fig. 373 *C*) the upper part of the wall of the sporangium, which contains no capillitium, becomes perforated in a sieve-like manner. In *Stemonitis* (Fig. 373 *A*) the whole peridium falls to pieces, and the capillitium is attached to a columella, which forms a continuation of the stalk. In *Fuligo varians* numerous sporangia are united to form a single cake-like brown fructification.

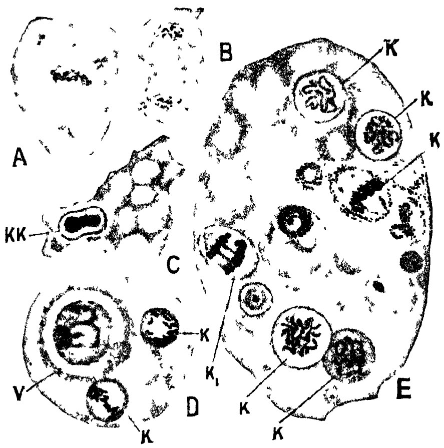


FIG. 376.—*Physarum didermoides.* *A*, *B*, Amoebae in process of division, *C*, conjugation of two haploid amoebae, *kk*, the two uniting nuclei; *D*, binucleate plasmodium with a haploid amoeba enclosed in a digestive vacuole; *E*, plasmodium with six dividing nuclei (k_1) and with digestive vacuoles. (After JAHN.)

The Myxomycetes are phylogenetically very primitive organisms, the swarm-spores and myxamoebae of which show connections with colourless Flagellatae, or more probably with Rhizopoda.

CLASSES XI AND XII

Fungi

The Fungi are plants which have true nuclei but NO CHROMATOPHORES. In the simplest families their thallus is naked and sometimes amoeboid; in all the more highly organised forms the cells are provided with a cell-wall which usually gives the reactions of chitin, but in some few cases of cellulose. The vegetative body may be unbranched or branched (Fig. 83), and may be unicellular or multicellular (septate). The individual filaments of a fungus are termed HYPHAE, while collectively they are spoken of as the MYCELIUM.

Some mycelia can survive unfavourable periods by the transformation of single cells of their hyphae into thick-walled resting-cells (gemmae); or tuberous associations of hyphae, so-called SCLEROTIA, may be formed.

ASEXUAL REPRODUCTION is effected by means of various kinds of spores. In forms living in water these may be naked, ciliated swarm-spores; in those inhabiting the land the spores have cell-walls and may be endogenous or exogenous in origin. SEXUAL REPRODUCTION takes place by the union of gametes (isogamy and oogamy), or of entire gametangia (gametangy) or of two cells of the thallus that are not differentiated as specific sexual cells (pseudogamy).

Fungi are saprophytic or parasitic. The majority of the saprophytes can be artificially cultivated. Glycogen and fat are widely distributed as reserve materials.

The Fungi are divided into two Classes. **Phycomycetes** (Algal Fungi) and **Eumycetes** (Higher Fungi).

CLASS XI

Phycomycetes (Algal Fungi) (1, 15, 51-60)

The thallus of the Phycomycetes is microscopically small and uninucleate in the lowest members of the Class; in the higher representatives it is well-developed, branched and multinucleate; with few exceptions in some of the highest developed forms, it is always tubular and without cross-septa. The diploid phase is restricted to the zygote.

Order 1. Archimycetes (53)

Olpidium brassicae, which lives as a parasite in the base of the stem of young Cabbage plants and causes their death, may be taken as a first example. It has uniciliate, oval swarm-spores which settle down on the host plant, surround themselves with a cell-wall and then pass their contents into a cell of the host. The protoplast of the fungus is at first naked and amoeboid, but soon forms a wall and grows into a unicellular multinucleate SPORANGIUM, lying in the cell of the host-plant; the zoosporangium forms a long projection which reaches the exterior, becomes mucilaginous at the tip, and gives egress to numerous uninucleate zoospores (Fig. 377). Unfavourable periods are tided over by THICK-WALLED RESTING-CELLS which probably arise by a SEXUAL PROCESS, as has been shown in the case of the related *Olpidium viciae*, which is parasitic on *Vicia unijuga*. In this the swarm-spores from over-ripe sporangia fuse in pairs; the biciliate naked zygote infects the host-plant in the same way as a zoospore, but forms a resting-cell instead of a sporangium. This, after fusion of the two sexual nuclei, germinates in the following spring by forming a beak-like process from which numerous zoospores escape. The latter, according to the external conditions, behave as asexual or sexual cells. The life history of *Synchytrium endobioticum*, the cause of the wart disease of the Potato, is similar. It gives rise to warty growths on the tubers and shoots of the host; these, which contain numerous resting-cells, later break down and decay.

Plasmodiophora brassicae (15), the cause of "Finger-and-Toes," probably belongs to the Archimycetes. This fungus has been usually placed in the Myxomycetes, but is distinguished from that group by the chitinous walls of its resting-cells. From each of these there develops a naked amoeboid protoplast; these swarm-spores penetrate the basal regions of species of *Brassica* and live as parasites in the cells. The stem and roots of the host plant exhibit tuberous swellings. In some way not yet clearly explained (there is probably a sexual process concerned) the parasite forms numerous resting spores in the cells, and these are set free by the decay of the tissues of the host.

Some members of the order live as spherical cells with a wall, on the outside of the host-plant; an example is afforded by *Rhizophidium pollinis* (Fig. 378) which obtains its nourishment by means of haustoria from pollen-grains of *Pinus* that have fallen into water. Only in the highest members of the group (for instance, *Polyphagus euglenae*, which is parasitic on cells of *Euglena*), is there a delicate branched mycelium which is unicellular and uninucleate.

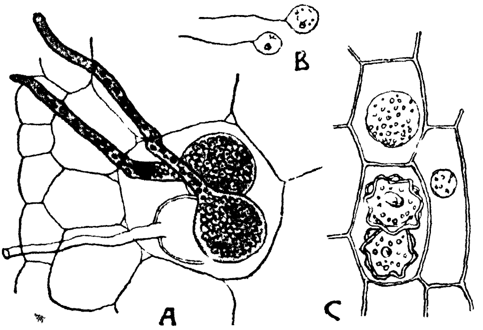


FIG. 377.—*Olpidium Brassicae*. *A*, Three zoosporangia, the contents of one of which have escaped (× 160) *B*, Zoospores (× 520). *C*, Resting sporangia (× 520) (After WORONIN.)

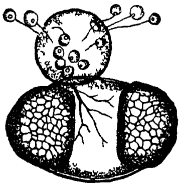


FIG. 378.—*Rhizophidium pollinis*. Zoosporangium on a pollen-grain. (After ZOPF.)

The Archimycetes are microscopically small, very simple, in part naked and amoeboid, less commonly filamentous fungi which live as parasites in the cells of other plants; the smallest live in the nuclei of the cells of *Amoeba*. They reproduce asexually by means of uni- or bi-ciliate swarm-spores and, so far as our knowledge goes, the sexual reproduction is by ciliated gametes; the whole vegetative body of the fungus is employed in the formation of the reproductive organ. When cell-walls are present they are composed of chitin.

It is very doubtful whether all the forms placed in this group are really related to one another. Probably they belong to a number of developmental series that are distinct in their phylogenetic origin.

Order 2. Oomycetes.

Family 1.—**Monoblepharidaceae** (^{54}). The species of *Monoblepharis*, composed of branched non-septate, multinucleate hyphae, live in water upon the decaying remains of plants. Asexual reproduction is effected by ZOOSPORES, which are formed in large numbers in club-shaped sporangia. The OOGONIUM, which is usually terminal, is separated from the rest of the thallus by a transverse wall and contains a single uninucleate egg-cell (Fig. 379). The ANTHERIDIA, similarly delimited by cell-walls, liberate a number of uniciliate spermatozoids; this is the only case in which spermatozoids are formed in the Fungi. A spermatozoid enters by an opening in the oogonial wall and fertilises the egg (Fig. 379); this now usually emerges from the oogonium and becomes a thick-walled spiny oospore.

2. The **Saprolegniaceae** (^{55}), live saprophytically on the surface of decaying plants and insects and even on living fishes. Asexual propagation is effected by club-shaped sporangia (Fig. 380) which produce numerous biciliate SWARM-SPORES. In *Saprolegnia*, which is easily obtained by leaving dead flies in water, these swarm-spores with terminal cilia withdraw the latter and become surrounded with a spherical wall; shortly afterwards, the contents again escape as bean-shaped zoospores with the cilia inserted laterally. These come ultimately to rest and, surrounding themselves with a wall, develop into a mycelium. In other genera there is only one type of swarm-spore. The sexual organs develop on older branches of the mycelium (Figs. 381, 382). The OOGONIA give rise to a larger or smaller number of egg-cells, rarely only to a single one. At first the oogonium contains numerous nuclei, most of which, however, degenerate, while the oospheres become delimited around the remaining nuclei. The egg-cells are always uninucleate. The multinucleate ANTHERIDIA do not form separate male cells, but apply themselves to the oogonia and send FERTILISING TUBES to the egg-cells. One male nucleus enters the egg-cell and fuses with its nucleus (Figs. 381, 382). The

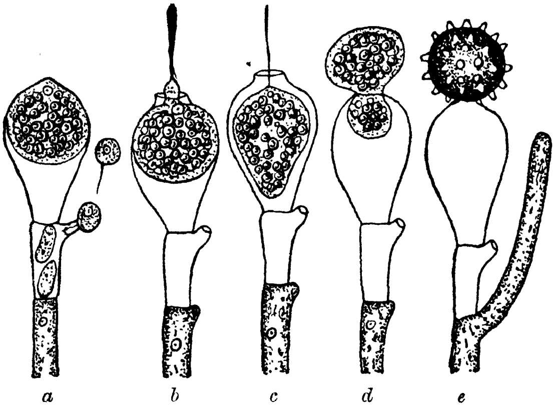


FIG. 379.—*Monoblepharis sphaerica*. *a*, End of a filament with an oogonium and, immediately beneath it, an antheridium from which the spermatozoids are escaping; *b*, a spermatozoid has entered the apical opening of the oogonium and is fusing with the egg-cell; *c*, the fusion completed; *d*, the fertilised egg escaping from the oogonium; *e*, oospore surrounded by a firm, spinose wall (from KNIEP, after WORONIN).

oospore after fertilisation acquires a thick wall. The reduction-division takes place on the germination of the oospore. In some forms the oospores develop parthenogenetically without being fertilised (Fig. 381 *op*). In *Saprolegnia* the asexual male and female organs occur on the same mycelium, their production being determined by changes in the nutritive conditions (cf. p. 309). *Saprolegnia* is thus monœcious ; diœcism also occurs in the family (*Dictyuchus monosporus*).

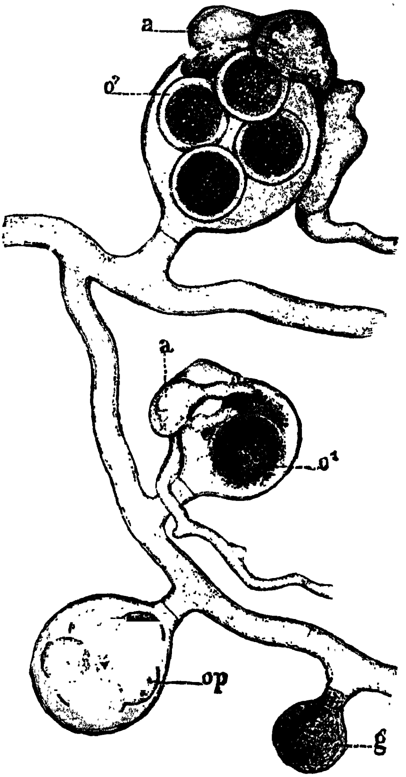


FIG. 381.—*Saprolegnia mixta.* Hyphae bearing the sexual organs : *a*, antheridium which has sent a fertilisation-tube into the oogonium; o^1, egg-cell ; o^2, oospore enclosed in a cell-wall ; *op*, parthogenetic oospores ; *g*, young oogonium. (After G. KLEBS.)

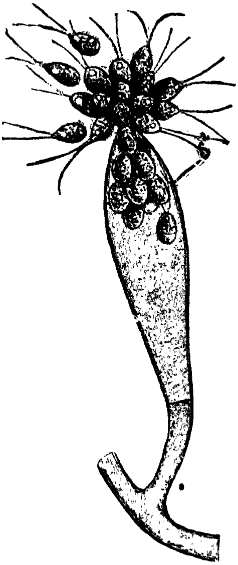


FIG. 380.—*Saprolegnia mixta.* The biciliate zoospores, s^2, are escaping from the sporangium. (After G. KLEBS.)

3. The Family **Peronosporaceae** ([56]) includes parasitic fungi which all live parasitically in higher land-plants. Thus *Plasmopara viticola* (Fig. 383) occurs as an intercellular fungus in the tissues of the leaves and fruits of the Vine, sending haustoria (Fig. 84) into the living cells. Branches of the mycelium grow out through the stomata forming a mould-like growth visible to the naked eye, which consists of the branched sporangiophores (Fig. 383) ; these bear numerous ZOOSPORANGIA. The sporangia are shed without opening and may be carried by the wind to the leaves of other plants ; they there liberate their contents, which have in the interval undergone division, as a number of biciliate swarm-spores. These germinate to form hyphae which enter the leaf.

The SEXUAL ORGANS are developed from the mycelium within the host plant. The oogonia form as swellings of the ends of hyphae, the antheridia as tubular outgrowths (Fig. 384). Both organs are cut off by cell-walls and contain numerous nuclei. All the nuclei except one in the oogonium collect at the periphery in the so-called periplasm; the single nucleus is situated at the centre of the large egg or oosphere, which is not sharply separated from the periplasm. The antheridium sends a process which opens at its tip into the oogonium and a single male nucleus enters the oosphere. The oosphere then becomes bounded by a wall and, after a time, the sexual nuclei fuse. The periplasm is utilised in the formation of the outer layer of the wall of the oospore. The latter germinates with a reduction-division

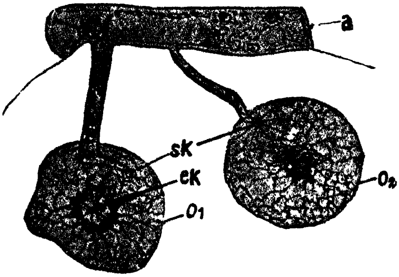


FIG. 382.—*Achlya polyandra*. The fertilisation of two egg-cells, *o*, of an oogonium by two tubes from the antheridium, *a*, *ek*, nucleus of the egg-cell, *sk*, male-nucleus; in o_2 the section has not passed through the egg-nucleus. (After TROW.)

In *Albugo Bliti* the oosphere contains numerous female nuclei which are fertilised by a corresponding number of male nuclei. The cytoplasm of

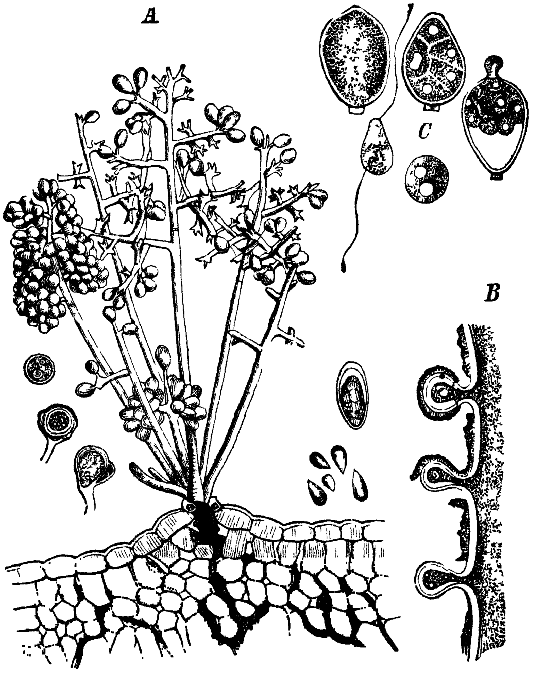


FIG. 383.—*Plasmopara viticola*. *A*, Sporangiophore emerging from a stoma. To the left, oogonium with antheridium and oospore. *B*, Haustoria. *C*, Liberation of zoospores from the zoosporangia. (From GAUMANN after MILLARDET.)

the oosphere, including all the fusion-nuclei, forms a cell-wall, so that the resulting structure is externally like a normal oospore, but contains many diploid nuclei.

In the Peronosporaceae a sharp differentiation of the gametes in the oogonium is thus lacking, as is the case for the male sexual cells in all the Oomycetes, with the exception of the Monoblepharideae.

The organs of asexual reproduction show an interesting ADAPTATION TO TERRESTRIAL LIFE. The most primitive members of the family (*e.g. Pythium gracile*, parasitic on *Vaucheria*) live permanently in water, and in them the zoospores escape from the zoosporangium without any separation of the latter from the hypha which bears it. On the other hand, in the forms parasitic on land-plants described above, the sporangia are shed. Since the escape of zoospores from these sporangia is dependent on moist weather a still higher adaptation is met with, for example,

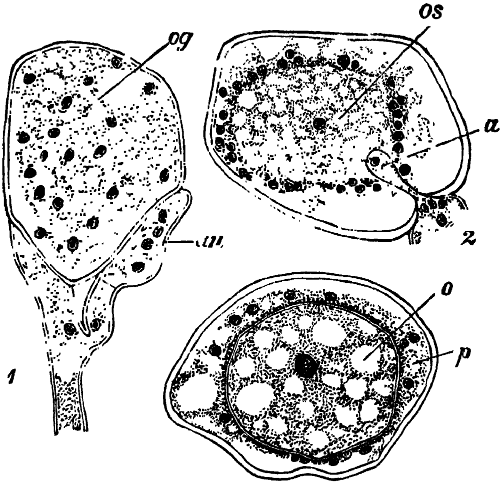


FIG. 384.—Fertilisation of the Peronosporeae. *1*, *Peronospora parasitica*. Young multinucleate oogonium (*og*) and antheridium (*an*). *2*, *Albugo candida*. Oogonium with the central uninucleate oosphere and the fertilising tube (*a*) of the antheridium which introduces the male nucleus. *3*, The same. Fertilised egg-cell (*o*) surrounded by the periplasm (*p*). (× 666. After WAGER.)

in *Peronospora*. Here the formation of zoospores is suppressed, and the whole sporangium germinates by sending out a germ-tube that can infect the host-plant. The sporangium has thus become a conidium. In *Phytophthora infestans* it depends on the external conditions whether the sporangium germinates by producing swarm-spores or by a germ-tube.

Many widespread diseases of plants are due to the Peronosporaceae. *Phytophthora infestans* causes the Late Blight of the Potato, a serious disease ; this can extend to the tubers, which become mummified. In the middle of last century this disease, which was introduced from America about 1830, became so extensive in wet seasons as to threaten the cultivation of the Potato. Another serious disease is the False Mildew of the Vine caused by *Plasmopara viticola*, which was introduced from America in 1878. In moist weather this appears epidemic on the leaves, which are prematurely shed, and the berries are also attacked and dry up. Since some 200 oospores, which can resist the winter conditions, are produced between the palisade cells of every square millimetre of surface of the leaves, it will be evident that the destruction of infected leaves in autumn is an important means of combating the disease. Recently a disease due to *Peronospora* has appeared on the Hop. First observed in Germany in 1923, it caused in 1926 in Bavaria alone, damage to the extent of 30 million gold marks. All these diseases spread as epidemics in wet weather, which favours the germination of the sporangia or conidia. In a particular case it has been estimated that 3 million sporangia were produced from each square centimetre of the leaf. They can be treated with good results by spraying the leaves with Bordeaux Mixture (a solution of copper sulphate and slaked lime), which hinders the germination of the sporangia.

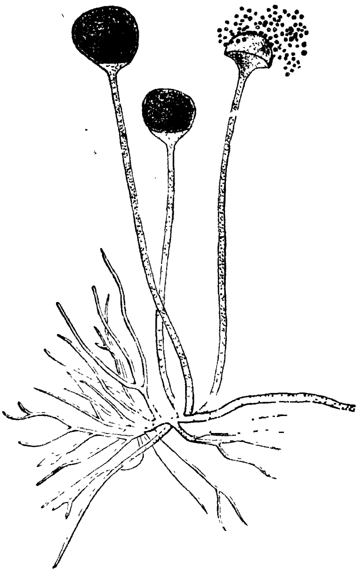


Fig. 385.—*Rhizopus nigricans.* Portion of the mycelium with three sporangia; that to the right is shedding its spores and shows the persistent hemispherical columella. (× 38.)

From what has been stated, it will be evident that the Oomycetes are filamentous, non-septate, branched, multinucleate fungi, which live as parasites or saprophytes. Their cell-walls give the reactions of cellulose. Those that inhabit the water (Monoblepharideae, Saprolegniaceae) reproduce asexually by ciliated zoospores; this method is replaced in the land-forms (Peronosporeae) by the distribution of entire sporangia or conidia. The sexual reproduction is oogamous. In the lowest representatives (*Monoblepharis*) the egg-cells are fertilised by motile spermatozoids; in all others the differentiation of male gametes is suppressed. Their function is taken over by male nuclei, which are carried from the antheridium to the oosphere by a fertilisation-tube. Further, the eggs are not always completely differentiated. In place of them in extreme cases a large number of female nuclei are present in the central portion of the ooplasm. After these have been fertilised by a corresponding number of male nuclei, the whole structure is surrounded by a cell-wall to form a multinuclear zygote.

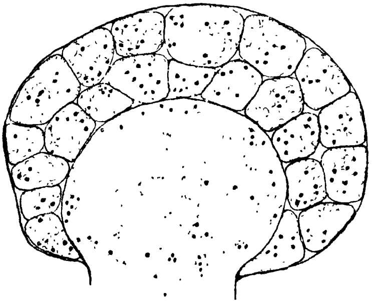


Fig. 386.—*Sporodinia grandis.* Median section of a ripe sporangium. The spores are multinucleate. (× 425. After Harper.)

Order 3. Zygomycetes.

1. The **Mucoraceae** (57) is a Family of terrestrial mould-fungi, which are for the most part saprophytic on vegetable or animal substances; less commonly they live as parasites.

One of the most widely distributed species is *Mucor mucedo*, the richly branched, non-septate mycelium of which forms a white fur-like growth on dung, bread, etc. From the nutritive hyphae in the substratum there arise vertically-growing branches, the sporangiophores, each of which bears a spherical SPORANGIUM; this is separated from the sporangiophore by a transverse wall which later bulges into the sporangial cavity forming the so-called columella (Figs 385, 387). The multinucleate protoplasm of the sporangium becomes divided by repeated cleavages to form numerous multinucleate spores, each of which is surrounded by a cell-wall. These escape by the swelling of a substance which lies between the spores and the consequent breaking up of the sporangial wall (Fig. 387). The spores may germinate at once, or later, for they remain for a long time capable of germination, to form a new mycelium. There appears to be no limit to the continuance of this by asexual reproduction.

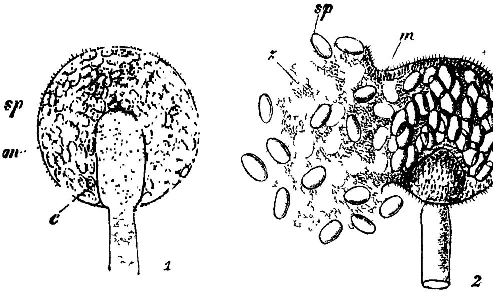


FIG. 387.—*1*, *Mucor Mucedo.* A sporangium in optical longitudinal section; *c*, columella; *m*, wall of sporangium; *sp*, spores. *2*, *Mucor mucilagineus.* A sporangium shedding its spores; the wall (*m*) is ruptured, and the mucilaginous substance (*z*) between the spores is greatly swollen. (*1*, × 225; *2*, × 300, from v. TAVEL, *Pilze.* After BREFELD.)

Mucor Mucedo is, as was first discovered by BLAKESLEE, dioecious; SEXUAL REPRODUCTION only takes place when two mycelia of different sex meet (57a). Since the sexual differentiation is entirely physiological and not in addition morphological, the two mycelia are distinguished as + and −. These form club-shaped branches, the ends of which come in contact owing to chemotropic influences, whereupon each cuts off a multinucleate GAMETANGIUM by a transverse wall; the gametangia are alike in form (Fig. 388, 1, 2). Gametes are not differentiated within these, but the + and − gametangia fuse to produce a zygospore with wart-like thickenings of the wall (Fig. 388, 4). Within this, the nuclei of distinct sexes are associated together and fuse in pairs. The reduction-division, with the determination of the sex of the nuclei, occurs in the germination, which takes place after a resting period.

In the germination of the zygote of most Mucoraceae, a sporangium is usually at once formed (Fig. 388, 5). The spores of this primary sporangium are generally (unlike those of the ordinary sporangia) uninucleate, so that some of them are + and others −.

The sexual processes in the other Mucoraceae are similar, though there are differences in details. Thus some species (*e.g. Sporodinia grandis*) have no sexual distinction but are monoecious; in other forms (*e.g. Absidia*) the gametangia are of different sizes, so that they can be distinguished as male and female.

The sporangia also are not always so typically constructed as in *Mucor Mucedo.* There are forms (*e.g. Thamnidium elegans*) in which, in addition to normal sporangia with many spores, there are others with a small number of spores, and even with only one, so that they become conidia. Some (*e.g. Chaetocladium*) have only conidia.

The species of *Pilobolus* have a peculiar method of spore-distribution. The whole sporangium is forcibly shot to a distance, that may amount to 2 metres, by means of the bursting of the highly turgescent sporangiophore. This ruptures just below the columella.

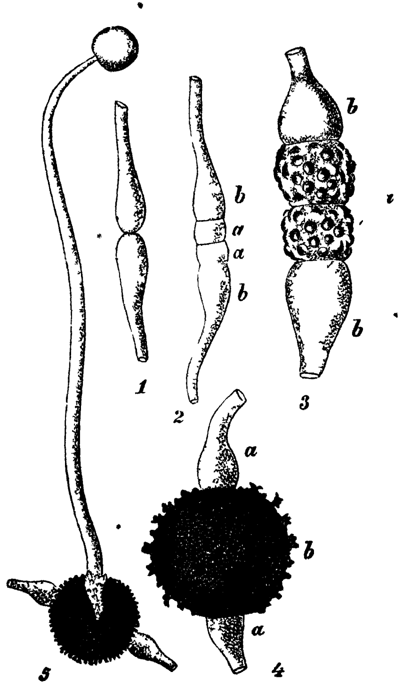


Fig. 388.—*Mucor Mucedo.* Different stages in the formation and germination of the zygospore. *1*, Two conjugating branches in contact; *2*, septation of the gametangia (*a*) from the suspensors (*b*); *3*, more advanced stage, the gametangia (*a*) are still distinct from one another; the warty thickenings of their walls have commenced to form; *4*, ripe zygospore (*b*) between the suspensors (*a*); *5*, germinating zygospore with a germ-tube bearing a sporangium. (*1-4*, × 225; *5*, × circa 60, from v. Tavel *Pilze.* After Brefeld.)

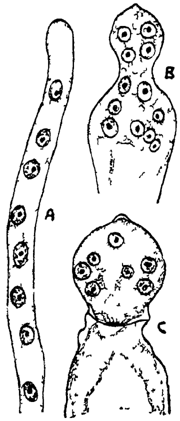


Fig. 389.—*Empusa muscae.* *A*, Hypha from the body of a fly. *B*, Young conidiophore arising from a hypha projecting from the body of the insect. *C*, Formation of the conidium into which the numerous nuclei have passed from the conidiophore. (× 450. After Olive.)

The sporangiophores of the majority of the Mucoraceae, especially those of *Phycomyces nitens*, are very sensitive phototropically.

Rhizopus nigricans (Fig. 385) with a brown mycelium with a creeping, runner-like growth, contains in its cell-sap substances that render it a fatal poison to animals (58).

2. The best-known example of the **Entomophthoraceae** (59) is *Empusa muscae* (Fig. 389). Its multinucleate conidia are homologous with the sporangia of the

Mucoraceae. The conidium gives rise to a germ-tube which penetrates the body of a fly and there develops to a parasitic mycelium, which leads to the death of the insect. From the dead body of the fly, which is often attached to a pane of glass, innumerable conidiophores project and forcibly abstrict conidia, which appear as a white halo on the glass around the insect. While sexual reproduction appears to be wanting in *Empusa muscae*, it is found in other species of the genus and in other Entomophthoreae (*Entomophthora, Conidiobolus*); the conjugation of multinucleate gametangia resembles the process in the Mucoraceae. Only in *Endogone* does fusion occur between a single male and a female nucleus.

The mycelium of the Entomophthoreae is to begin with unicellular, but sooner or later becomes multicellular by the formation of transverse walls In *Basidiobolus* (60) the mycelium is septate from germination onwards, *B. ranarum* occurs in the alimentary canal and on the excrement of frogs

The Zygomycetes are mostly saprophytic fungi with a much-branched mycelium. This is non-septate and multinucleate in the Mucoraceae, but septate in the Basidiobolaceae; the cell-walls are composed of chitin. The asexual reproduction is adapted to terrestrial conditions, though in a somewhat different way from that found in the Oomycetes. In the latter the whole sporangium was separated, and gave rise to zoospores at the place where it germinated. In the Zygomycetes it is the zoospores themselves that are transformed into resistant structures enclosed by cell-walls and capable of being transported by the air. On the other hand, the progressive reduction of a sporangium to a conidium is met with in the Zygomycetes as well as in the Oomycetes. In the process of sexual reproduction gametes are never formed; conjugation always takes place between entire multinucleate gametangia, which are usually alike, to form a multinucleate zygote.

The phylogeny of the Phycomycetes is still obscure.

The name Algal Fungi is based on the resemblance in structure of the thallus and in the sexual organs which many Oomycetes show to certain Chlorophyceae (Siphonales); the Oomycetes have been regarded as Algae which have become colourless. The Archimycetes on this view would be reduced forms. It is possible, however, to regard the Archimycetes as related to the Myxomycetes and Flagellatae, and to derive the Phycomycetes from them with *Polyphagus* as a connecting link. It is doubtful, however, whether this indicates a real relationship.

It is very probable that the Phycomycetes are a heterogeneous and artificial group, which will in the future be broken up. On this view the Phycomycetes would be polyphyletic.

Key to the Orders of Phycomycetes (with few exceptions Fungi with a non-septate mycelium):

Archimycetes: Parasites; usually naked, rarely provided with a chitinous cell-wall; rarely filamentous; with zoospores and planogametes.

Oomycetes: Mycelium, filamentous, branched, non-septate with a cellulose wall; zoosporangia, or asexual reproductive organs derived from these; oogamy; mainly parasites.

Zygomycetes: Filamentous, almost always non-septate mycelium, with wall composed of chitin; no zoospores; sexual reproduction by the conjugation of multinucleate gametangia; saprophytes or parasites.

CLASS XII

Eumycetes. (Higher Fungi) (1, 7, 51, 52, 61-86)

The Eumycetes are terrestrial fungi and, with the exception of certain reduced groups, have a richly branched mycelium composed of septate hyphae with chitinous walls. The ASEXUAL SPORES, according to the Sub-Class, are developed within asci or on basidia. The ASCUS is characteristic of all Ascomycetes; it is a tubular sporangium, which gives rise endogenously, by free cell-formation, to a definite number of spores (usually eight) (Fig. 390). The more or less club-shaped BASIDIUM of Basidiomycetes abstricts exogenously a definite number of spores (usually four) (Fig. 412). Both in the ascus and the basidium there is a fusion of two nuclei, followed by a REDUCTION-DIVISION before spore-formation.

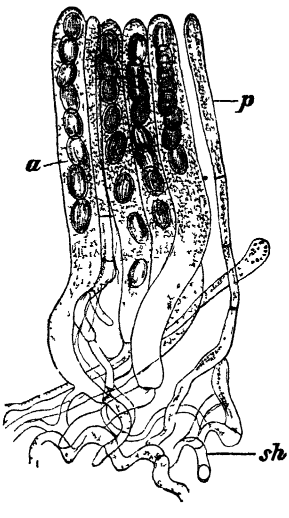


FIG. 390 —Portion of the hymenium of *Morchella esculenta.* *a*, Asci, *p*, paraphyses; *sh*, subhymenial tissue (× 240. After STRASBURGER.)

Asci and basidia are usually developed in special fructifications composed of interwoven hyphae (plectenchyma, Fig. 36). They usually form a definite layer, the HYMENIUM, in which they stand side by side. CONIDIA, formed without any relation to a reduction-division, occur as accessory means of reproduction, especially in the Ascomycetes.

Sub-Class I.—Ascomycetes (1, 7, 51, 52, 61-74, 89, 90)

A. Protoascomycetes (61a)

As an example of a lowly organised Ascomycete, *Eremascus fertilis*, which was found on opening a pot of jelly, may be taken. It belongs to the Order **Endomycetales.** Its multinucleate hyphae form uninucleate beak like branches which fuse with one another by their summits (Fig 391 1), the two sexual nuclei fusing (391 3). The region connecting the two sexual branches in which the fusion nucleus lies is now delimited by transverse walls and enlarges to form a spherical structure. The diploid fusion-nucleus divides, with reduction in the number of chromosomes, to give rise to eight haploid nuclei which become surrounded by protoplasm and cell-walls and transformed into eight spores (Fig. 391 4). Thus, in this case, an eight-spored ascus arises directly from the zygote. In related genera there is a fusion of multinucleate gametangia.

In some species of *Endomyces* the mycelium readily breaks up into chains of conidia, and this forms a connection with the family **Saccharomycetes** (73), Yeast-fungi. Only a few species (*Saccharomyces Ludwigii*) are able, under special nutritive conditions, to still form true hyphae. The majority are unicellular, the spherical, oval, or cylindrical cells being uninucleate and multiplying by a process of BUDDING (Fig. 392, cf. p. 25). SEXUAL REPRODUCTION has been observed in *Schizosaccharomyces* and some other genera; two cells conjugate and form an ascus which at first contains the diploid fusion-nucleus (Fig. 393). In this, as a result of nuclear division, eight haploid spores are developed and they become free by the rupture of the wall of the ascus. The spore germinates to form a vegetative cell which buds. In many Yeasts the ascus contains only four spores, which in most cases (*Saccharomyces cerevisiae*, *S. ellipsoideus*) arise parthenogenetically, without previous conjugation, in the haploid cell. Spore-production may be wanting (asporogenous yeasts).

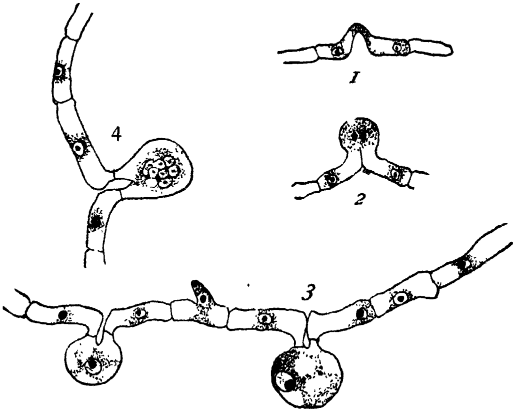


Fig. 391.—*Eremascus fertilis.* 1, 2, Conjugation; 3, Delimitation of the zygote by cell-walls, the nuclei having fused to give the diploid fusion-nucleus; 4, Mature ascus with eight young spores. (After Guilliermond, from Kniep.)

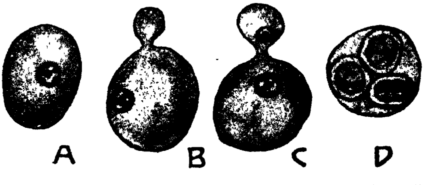


Fig. 392.—*Saccharomyces cerevisiae.* *A*, Yeast-cell; *B*, *C*, yeast-cell budding; *D*, ascus with four spores. (× 1125. After Guilliermond.)

The Yeasts are thus a family of fungi which shows great reduction both as regards the vegetative structure and the sexual reproduction.

Yeast fungi occur on fruits, in mucilaginous exudations and similar situations in Nature, and give rise to alcoholic fermentation of sugary solutions (p. 271). The Wine-yeast (*Saccharomyces ellipsoideus*) passes the winter in the soil in the form of spores and then reaches the surface of the grapes and need not be added to the grape-juice. The Beer-yeast (*Saccharomyces cerevisiae*) is only known in the cultivated form. Both species occur in a number of distinct races, which are grown in pure cultures and employed in fermentations. Most yeasts are colourless but some kinds have a red colour.

It is characteristic of all Protoascomycetes, as has been seen in the examples described, that the ascus is formed directly from the zygote. Neither fructifications nor other complications appear on the simple mycelium.

B. Euascomycetes

As a typical example of the method of reproduction ([61, 69]) of the Euascomycetes, *Pyronema confluens* may in the first instance be described. This fungus occurs on the old sites of fires in woods, where it forms pink lens-shaped fructifications a few millimetres in diameter. In the development of a fructification the terminal cells of certain branched hyphae enlarge to form spherical multinucleate structures which are the female gametangia or ascogonia; each ASCOGONIUM bears at its summit an elongated, curved, multinucleate papilla, termed the TRICHOGYNE. In the immediate neighbourhood of the ascogonia and from the same hyphae club-shaped multinucleate ANTHERIDIA are developed. The sexual organs thus arise in groups (Fig. 394 *A*). The tip of the trichogyne becomes applied to the antheridium, and an opening forms between them. The nuclei of the trichogyne degenerate, while the male nuclei pass by way of the trichogyne into the ascogonium; the separating wall breaks down to allow of this and is again formed. There are now in the ascogonium numerous female and numerous male nuclei, and these become associated in pairs but do not fuse (*C*). A number of outgrowths now arise from the ascogonium and form the ASCOGENOUS HYPHAE into which the pairs of nuclei pass. The ascogenous hyphae grow and branch, and the pairs of nuclei increase in number by conjugate division, *i.e.* simultaneous division of the male and female nuclei of the pair. Cell-walls form, giving rise to cells each of which contains two nuclei of unlike sex. An ascus is formed from each of the terminal cells of the branches in the following way. The tip of the cell curves backwards to form a stalked hook (Fig. 395 *A*) and the pair of nuclei undergo conjugate division; two nuclei of different sex remain near the summit, while one nucleus passes into the tip of the hook and another into the stalk (*s*). The stalk and tip are cut off from the summit of the hook by cross-walls, giving a three-celled structure (Fig. 395 *B*) composed of two uninucleate and one binucleate cell. The latter is the young ascus, and in it at last NUCLEAR FUSION takes place, the cell enlarging as a uninucleate diploid ASCUS (*C*). There

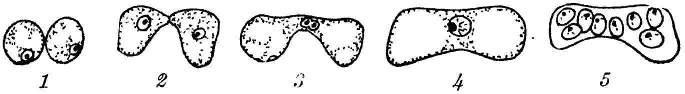


FIG. 393.—*Schizosaccharomyces octosporus.* 2, beginning of conjugation; 3, fusion of nuclei; 4, diploid nucleus in the ascus; 5, ascus with eight spores. (After GUILLIERMOND, from GAUMANN.)

are now formed by three successive divisions, in which reduction takes place, eight nuclei, and around these by free cell-formation (p. 25) the eight haploid ASCOSPORES delimited by cell-walls arise (Fig. 395 *D*).

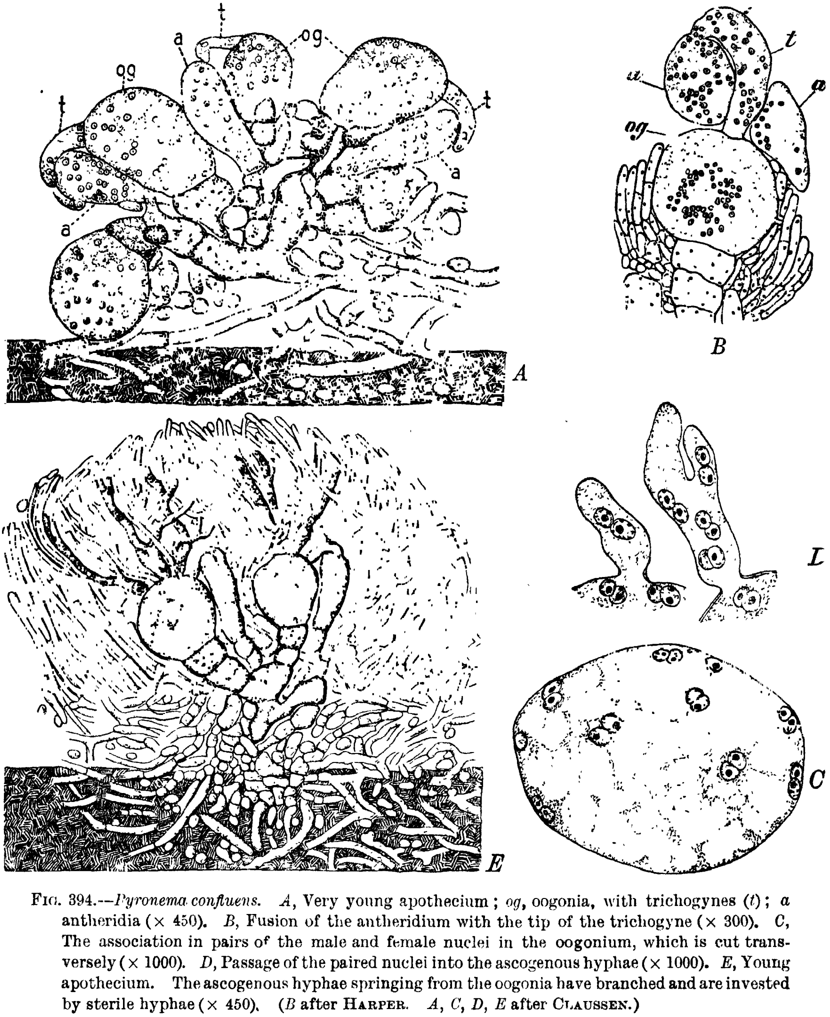


FIG. 394.—*Pyronema confluens.* *A*, Very young apothecium; *og*, oogonia, with trichogynes (*t*); *a* antheridia (× 450). *B*, Fusion of the antheridium with the tip of the trichogyne (× 300). *C*, The association in pairs of the male and female nuclei in the oogonium, which is cut transversely (× 1000). *D*, Passage of the paired nuclei into the ascogenous hyphae (× 1000). *E*, Young apothecium. The ascogenous hyphae springing from the oogonia have branched and are invested by sterile hyphae (× 450). (*B* after HARPER. *A*, *C*, *D*, *E* after CLAUSSEN.)

In this process all the protoplasm is not used up, so that the spores lie embedded in the remaining periplasm in the ascus.

Meanwhile the hook-cell has fused with the stalk-cell and passed its nucleus into the latter. This reconstitutes a binucleate, cell from which another ascus can originate. In this way clusters of asci may arise at the end of an ascogenous branch.

Even at the period of the union of the sexual organs they are surrounded by a loose investment of haploid, investing hyphae (Fig. 394 *B*). These increase as the ascogenous hyphae are growing (Fig. 394 *E*) and form the fructification. The sterile hyphae give off branches which, as the PARAPHYSES (Fig. 360), form along with the asci a superficial layer called the HYMENIUM (Fig. 403). The ascospores, on the opening of the ascus at its tip, are actively ejected by the swelling of the periplasm ; they are then carried by currents of air and give rise to new plants (^{64}).

The characteristic feature of this process is that nuclear-fusion does not at once follow the conjugation of the gametangia. The fusion of the protoplasm and the nuclear-fusion are here widely separated from one another, both in space and time, by the stage with conjugate nuclei.

There are many deviations from the type of life-history just described ($^{62, 63}$), and these will be mentioned, where necessary, in the succeeding description of the Orders. In some Families sexuality is almost or completely lost, so that the asci are produced without any preceding fertilisation. Some species (*e.g. Penicillium luteum*, *Ascobolus magnificus*) are dioecious, the antheridia and ascogonia being produced on sexually different mycelia.

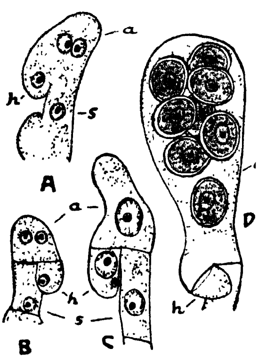


FIG. 395.—Development of the Ascus. *A-C*, *Pyronema confluens*. (After HARPER.) *D*, Young ascus of *Boudiera* with eight spores. (After CLAUSSEN.) Explanation in text.

The form of the fructifications is of great importance in distinguishing the Orders of Ascomycetes.

Order 1. Plectascales ($^{66, 67}$)

These have CLOSED SPHERICAL FRUCTIFICATIONS.

The best known representatives are two common moulds, *Aspergillus herbariorum* and *Penicillium crustaceum*. They occur on the most various organic substrata such as bread, fruits, leather, cheese (*Penicillium Roquefortii* occurs in Roquefort cheese). The white mycelium bears closely crowded short conidiophores with bluish-green conidia. In *Aspergillus* (Fig. 396) the end of the conidiophore is swollen and bears short sterigmata radiating on all sides from the spherical surface ; from these sterigmata bead-like rows of conidia (*c*) are abstricted. The spores of *Penicillium* are in similar rows but arise on branched conidiophores (Fig. 396).

The SEXUAL ORGANS, which make their appearance later than the conidia, are more simply constructed than those of the example described in the introduction above. In *Aspergillus* the ascogonium is spirally twisted and without any trichogyne that is externally recognisable ; the finger-like antheridia grow in contact with it (Fig. 307 *B*). In some species of *Penicillium* the two gametangia are of similar form and twist round one another spirally (Fig. 397 *A*). There are also forms (*Monascus purpureus*) in which the ascogonium has a trichogyne. The asci are usually spherical and lie IRREGULARLY within a closed fructification (PERITHECIUM) which is spherical and about the size of a pin-head. The wall of this (PERIDIUM) is formed of closely-associated hyphae, and the spores only become free when it has broken down.

Elaphomyces cervinus has brown truffle-like perithecia that may attain the size of a walnut; it grows below the surface of the soil in pine woods.

Order 2. Erysiphales (Mildew Fungi) ([7, 51 65])

The Erysiphales are parasitic fungi; their perithecia resemble those of the preceding order, but the asci, instead of being irregularly placed, stand singly or in a group within the fructification.

The Mildew Fungi (Fam. **Erysiphaceae**) have a mycelium that grows like a spider's web on the leaves of higher plants, sending haustoria into the epidermal cells of the host. They are spread during the summer by means of CONIDIA which are abstricted in a row from erect branches of the mycelium and carried by the wind (Fig. 398 *A*). The ANTHERIDIUM and ASCOGONIUM are always uninucleate; there is no trichogyne. The ascogenous hyphae are often only slightly developed, and in some cases only a single ascus is produced. There are often only four or two ascospores in the ascus, instead of eight. The small dark PERITHECIA, provided with peculiar, variously formed appendages, lie as closed spheres in the white mycelium on the leaves; they are organs which tide the fungus over the winter (Fig. 398).

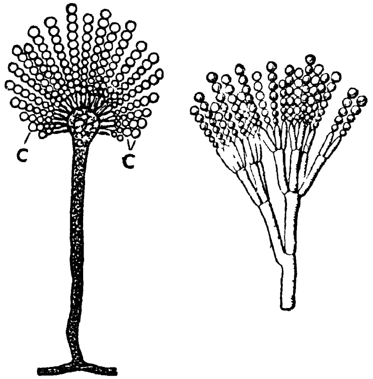


FIG. 396.—Conidiophores of *Aspergillus herbariorum* (left) and *Penicillium crustaceum* (right).

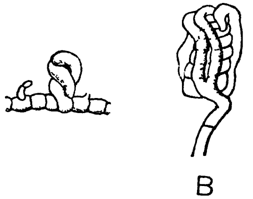


FIG. 397.—A, *Penicillium, crustaceum*, spirally twined gametangia. B, *Aspergillus herbariorum*, cork-screw-like ascogonium with antheridia applied to it (mag. after KNY and DE BARY from GÄUMANN).

The mildew fungus of the Vine occurs on the leaves and berries of *Vitis* in America, and has appeared in Europe as an injurious parasite of the Grape-Vine since 1845. This fungus, known as *Oidium Tuckeri*, is the conidial form of *Uncinula necator*, the small perithecia of which have appendages spirally rolled at their free ends and are only rarely met with. The fungus is treated by powdered sulphur. Other cultivated plants are injured by Mildew Fungi, *e.g.* the Oak by *Microsphaera quercina* and the Gooseberry by *Sphaerotheca mors uvae.*

Order 3. Pyrenomycetales

The Pyrenomycetes comprise an exceedingly varied group of Fungi, some of which are parasitic upon different portions of plants, and others are saprophytic upon decaying wood, dung, etc., while a few genera occur as parasites upon the larvae of insects. The FLASK-SHAPED fructifications or PERITHECIA are characteristic of this order. The perithecia are open at the top, and are covered inside, at the base, with a hymenial layer of asci and hair-like paraphyses (Fig. 399). The ascospores escape from the perithecia through the aperture.

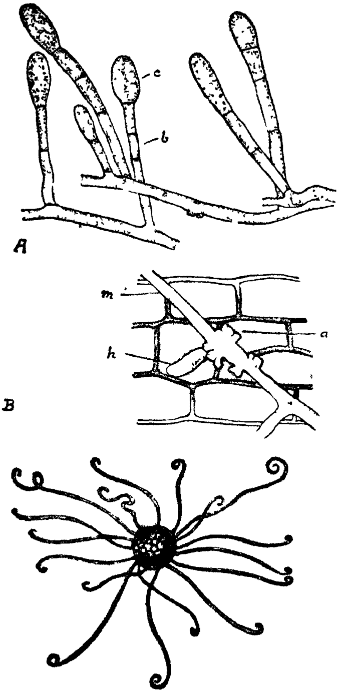


FIG. 398.—*Uncinula necator*. *A*, Conidial stage; *c*, conidium; *b*, conidiophore. *B*, Hypha which has formed a disc of attachment (*a*) and has sent a haustorium (*h*) into an epidermal cell. *C*, Perithecium with appendages. (From SORAUER, LINDAU, and REH. *Handb. d. Pflanzenkrankheiten*, ii. p. 194. 1906.)

The simplest Pyrenomycetes possess free perithecia (Fig. 399) which are usually small and of a dark colour, and grow singly on the inconspicuous mycelium (*e.g. Podospora*). In other cases the perithecia are in groups embedded in a cushion- or club-shaped, sometimes branching, mass of compact mycelial hyphae having a pseudo-parenchymatous structure. Such a fructification is known as a STROMA. In some the conidia are also produced in flask-shaped structures which are called PYCNIDIA (Fig. 400).

The club-shaped stromata of *Xylaria hypoxylon*, with perithecia below and a white covering of conidia on the simple or branched apical end, are commonly found on stumps of Beech. *Nectria galligena* is a very injurious parasite in the cortex of some trees and causes the Canker of fruit-trees; its numerous, small, red perithecia are formed in winter and spring (68).

Claviceps purpurea, the fungus of Ergot, is important on account of its official value. It is parasitic in the young ovaries of different members of the Gramineae, particularly of Rye. The ovaries are infected in early summer by the ascospores. The mycelium soon begins to form conidia, which are abstricted in small clusters from short lateral conidiophores (Fig. 401 *A*). At the same time a sweet fluid is extruded. This so-called HONEY-DEW is eagerly sought by insects, and the conidia embedded in it are thus carried to the ovaries of other plants. After the completion of this form of fructification, and the absorption of the tissue of the ovary by the mycelium, a sclerotium is eventually formed in the place of the ovary from the hyphae of the mycelium by their intimate union, especially at the periphery, into a compact mass of pseudo-parenchyma (Fig. 35). These elongated dark-violet SCLEROTIA, which project in the form of slightly curved bodies from the ears of Rye, are known as Ergot, SECALE CORNUTUM (Fig. 401 *B*). The sclerotia, copiously supplied with reserve material (fat), eventually fall to the ground, where they pass the winter, and germinate in the following spring when the Rye is again in flower. They give rise to bundles of hyphae which produce long-stalked, rose-coloured globular heads (*C*). Over the surface of the latter, numerous sunken perithecia (*D*, *E*) are distributed.

Multinucleate antheridia and ascogonia are developed, and these conjugate. Each perithecium contains a number of asci with eight long, filiform ascospores, which are ejected and carried by the wind to the inflorescences of the grass

OFFICIAL —Ergot is the sclerotium of *Claviceps purpurea*

Order 4 Discomycetales (69)

The Discomycetes are connected by intermediate forms with the Plectascales Their asci are arranged in a flattened hymenium within the young fructification which is later opened by the widening of the upper region The result is an open cup or saucer shaped structure (APOTHECIUM) bearing the asci on its upper surface (Figs 402, 403)

The reproductive story was given in the introduction for *Pyronema confluens* (p 444) In many Discomycetes a reduction in the sexual organs is found, associated with loss of sexuality The antheridia may be functionless or entirely suppressed, in extreme cases the ascogonia are wanting, and in their place only a coil of hyphae can be recognised The ascogenous hyphae can, however, always be demonstrated in the young fructification The absence of the antheridia leads to peculiar relations in *Ascobolus carbonarius*, its elongated trichogyne grows towards certain conidia, which have taken over the function of the antheridium

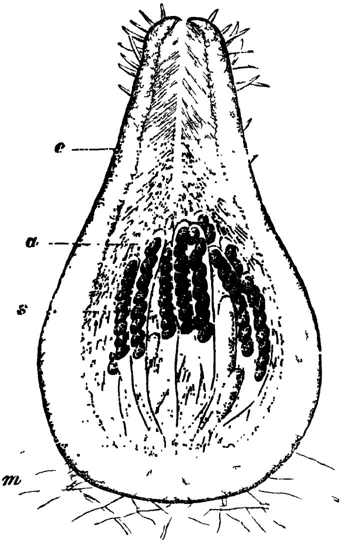


FIG 399 —Perithecium of *Podospora fimiseda* in longitudinal section s Asci a paraphyses e periphyses m mycelial hyphae (× 90 After v TAVEL)

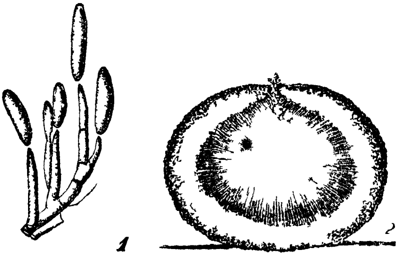


FIG 400 —*1* Conidiophore abstricting conidia from a pycnidium of *Cryptospora hypodermia* (× 300 After BREFELD) *2* Pycnidium of *Strickeria obducens* in vertical section (× 70 After TULASNE)

Peculiarities are exhibited by the sexual organs of some Discomycetes which are associated with Algae to form Lichens (cf p 474) Free, male sexual cells are found in these cases These SPERMATIA are small, spherical cells formed by abstriction from the ends of hyphae (90) in SPERMOGONIA (resembling that shown in Fig 428), which are sunk in the Lichen thallus. The spermatia emerge from the spermogonia embedded in mucilage and when they come in contact with a trichogyne adhere to it (89) The trichogynes are very long (Fig 404) and formed of a row of cells, each arises from a coiled multicellular ascogonium and projects above the surface of the thallus After dissolution of the wall at the point of contact (Fig 404 *B*) the

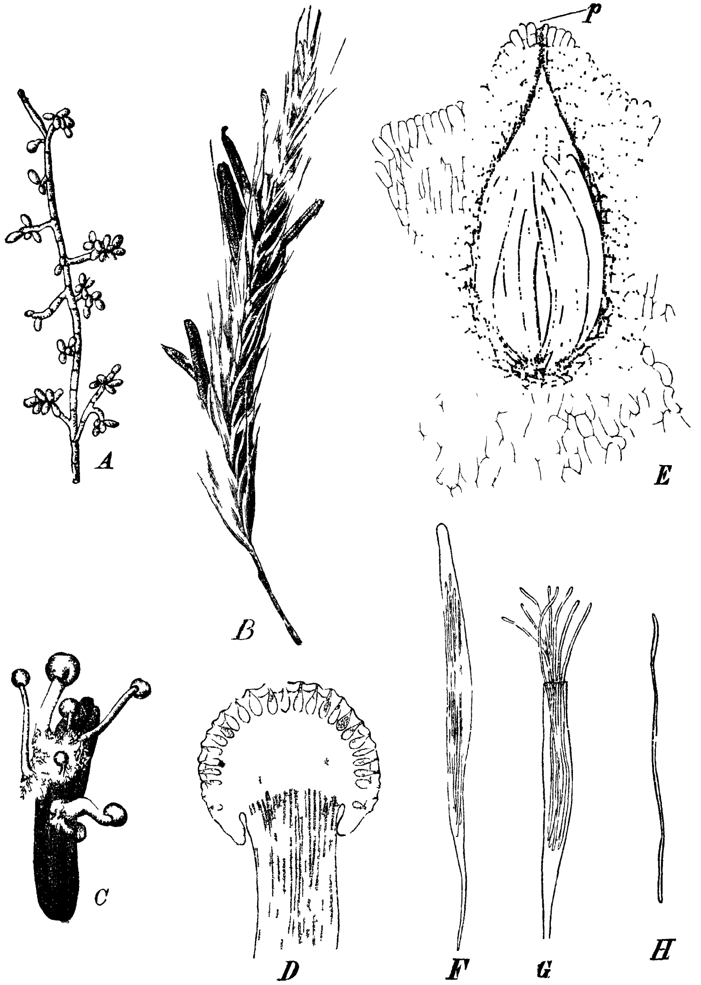


Fig 401 —*Claviceps purpurea* *A* Mycelial hyphae with conidia *B* ear of Rye with several ripe sclerotia *C* a sclerotium with stromata *D* longitudinal section of a fructification showing numerous perithecia *F* a single perithecium more highly magnified *F* ascus with eight filiform spores *G* a ruptured ascus with escaping spores *H* a single spore (*A* after Brefeld *C*–*H* after Tulasne *B* photographed from Nature Official and Poisonous)

nucleus of the spermatium disappears, the transverse walls of the trichogyne become swollen, and the middle cells of the ascogonium grow out into ascogenous hyphae The passage of the male nucleus into the trichogyne has only been monstrated in one case, and nothing is known as to its relation to the ogonium.

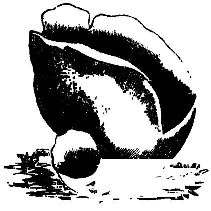


FIG. 402.—*Peziza aurantiaca.* (Nat. size. After KROMBHOLZ.)

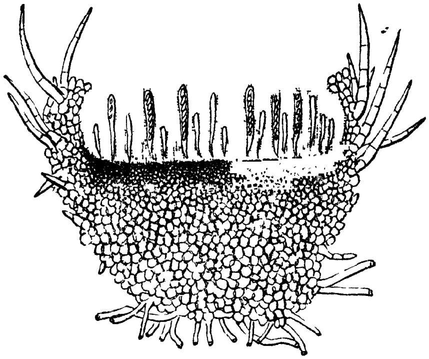


FIG. 403.—*Lachnea pulcherrima.* Apothecium ruptured, showing old and young asci between the paraphyses (After WORONIN, from v. TAVEL.)

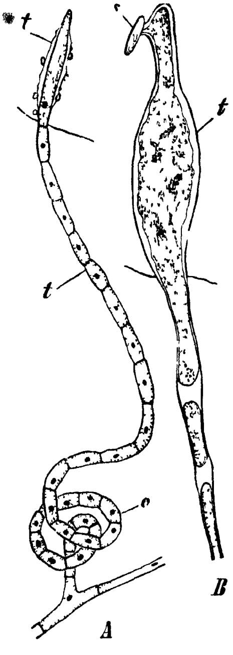


FIG. 404.—*Collema crispa* *A*, carpogonium (*c*) with its trichogyne (*t*) (× 405). *B*, apex of the trichogyne with the spermatium (*s*) attached (× 1125). (After E. BAUR.)

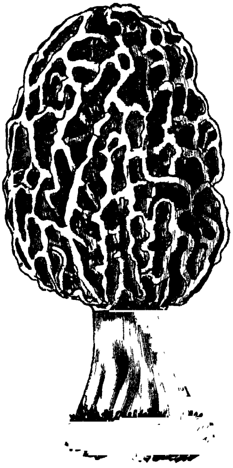


FIG. 405.—*Morchella esculenta.* (½ nat size.)

In *Collema pulposum* the spermatia are not shed from the hyphae which bear them. The long trichogynes remain within the thallus and grow towards the spermatia with which fusion takes place (^{90}).

In exceptional cases the spermatia of these Lichen fungi can germinate and form a small mycelium. Some conclude from this that they are conidia which—as in *Ascobolus carbonarius*—have taken over the function of the antheridia which have been lost in the course of evolution.

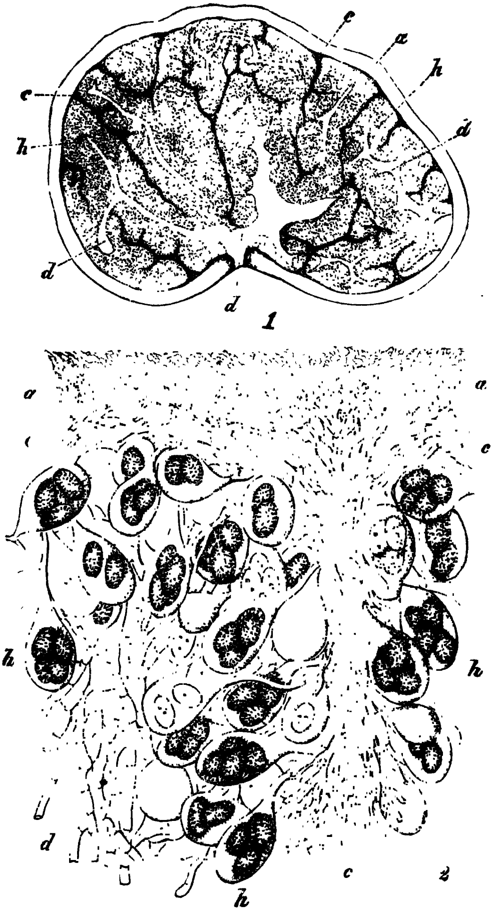


FIG. 406.—*Tuber rufum.* *1*, A fructification in vertical section (× 5); *a*, the cortex; *d*, air-containing tissue; *c*, dark veins of compact hyphae; *h*, ascogenous tissue. *2*, A portion of the hymenium (× 460). (After TULASNE, from V. TAVEL, *Pilze.*)

Relatively few Discomycetes live in lichen thalli. The majority occur on and in dead or living parts of plants, especially on rotting wood but also in humus soils. They form apothecia which are usually small (*e.g.* *Pyronema*), but less frequently (*e.g.* *Peziza aurantiaca*, Fig. 402) may attain the width of a decimetre.

In the Family **Helvellaceae**, the members of which live in the soil, the fructification is stalked and only when young is cup-shaped; later the hymenium becomes convex so that the asci are directed outwards. In some cases the hymenium becomes thrown into folds (Fig. 405) as in *Gyromitra esculenta*, and still more markedly in *Morchella esculenta*, the edible Morchella fungus, which attains a height of 12 centimetres (70, 70a).

In some Discomycetes (*Sphaerosoma*) the fructifications are subterranean and tuberous, and have the hymenium on the outer surface, which may be folded or pitted. These forms lead on to the next order.

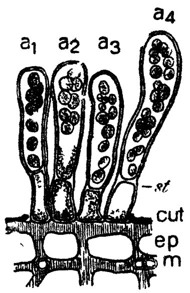


Fig. 408.—*Taphrina Pruni*. Transverse section through the epidermis of an infected plum. Four ripe asci, a_1, a with eight spores, a_3, a_4 with yeast-like conidia abstricted from the spores; *st*, stalk-cells of the asci; *m*, filaments of the mycelium cut transversely; *cut*, cuticle; *ep*, epidermis. (× 400. After SADEBECK.)

Order 5. Tuberales (Truffles) (71)

The simplest forms of this order are comparable to a *Sphaerosoma* with very deep pitting or folding of the surface. In higher forms the openings of the canals lined by the hymenium become obscured. The asci thus lie in chambers or tracts within the tuberous subterranean fructification. These are known as truffles, and some of them are valuable edible fungi (70), *e.g. Tuber brumale*, *T. melanosporum* (Perigord Truffle), etc. The mycelium of the Tuberaceae lives saprophytically in the soil of woods and that of some of them forms mycorrhiza (p. 261).

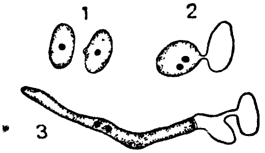


Fig. 407.—*Taphrina epiphylla*. 1, 2, conjugation of conidia; 3, germ-tube with the two nuclei derived from the gametes. (After WIEBEN, from KNIEP.)

Order 6. Exoascales (72)

The single Family (**Exoasceae**) contains only the genus *Taphrina*, the species of which live as parasitic fungi in various trees. As annual fungi they may attack the leaves and cause diseases of these, or the mycelium may persist over the winter in the tissue of the host-plant and give rise to an annually recurring disease. The presence of the mycelium in the tissues of the infected part causes the abnormally profuse development of branches known as WITCHES'-BROOMS. *Taphrina carpini* produces the abnormal growths occurring on the Hornbeam; *Taphrina cerasi* those on Cherry trees. *Taphrina deformans* attacks the leaves of the Peach and causes them to curl. *Taphrina pruni* is parasitic in the young ovaries of many species of *Prunus*, and produces the malformation of the fruit known as "Bladder Plums," containing a cavity, the so-called "pocket," in the place of the stone; the mycelium persists through the winter in the branches.

Ascogonia and antheridia are not known in *Taphrina* and the condition with paired nuclei arises in the following way. The ascospores exhibit a yeast-like budding and give rise to numerous conidia, frequently while still within the ascus (Fig. 408 a_3, a_4), or on the spores being sown in water or sugary nutrient solutions. The spores are of different sexes and the conidia budded off from them conjugate in pairs by means of a conjugation-tube (Fig. 407), through which the nucleus passes from one of the conidia into the other. The latter grows out as a mycelium with paired nuclei which infects the host-plant. The asci, containing eight spores, project from the epidermis of the leaves in a continuous layer, without paraphyses (Fig. 408). Reduction-division and determination of sex take place on the division of the primary diploid nucleus in the young ascus; four of the resulting ascospores belong to the one sex and four to the other.

The Exoasceae are to be regarded as reduced Ascomycetes. They have no fructifications and no conidia are formed on the mycelium; in place of these there is the budding of the ascospores.

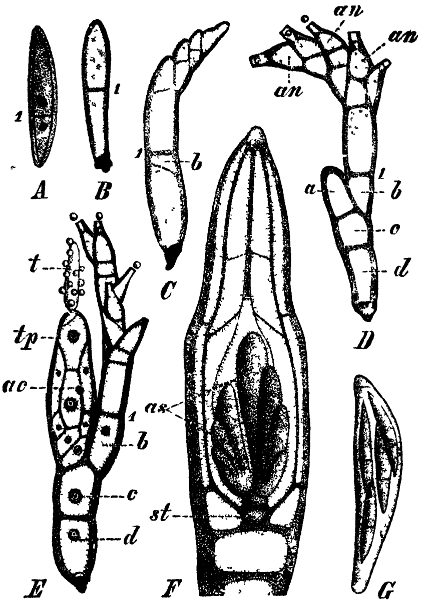


Fig. 409.—*Stigmatomyces Baerii.* Description in text. *A*, Spore. *B F*, Successive developmental stages. *D*. With spermatia escaping from the antheridia *an*. *E*. With antheridia above and the lateral female-organ, *F*, Perithecium with developing asci. *G*, Ripe ascus. (After THAXTER.)

Order 8. Laboulbeniales (74)

The Laboulbeniales live as parasites on insects, from the bodies of which their minute fructifications project like bristles that are at most 1 millimetre in length. While some send hyphae into the insect's body, the majority are attached to the exterior of the chitinous covering. One of the best-known examples is *Stigmatomyces Baerii* which occurs on house-flies. The two cells of the ascospore, after it has become attached to the body of the fly, undergo divisions (Fig 409 A-C). From the upper cell an appendage is developed, bearing several unicellular ANTHERIDIA (D, *an*) from which spherical, naked non-ciliated SPERMATIA are shed. The lower cell first divides into four cells (D, *a*, *b*, *c*, *d*), and of these the cell *a* projects and gives rise to the multicellular female structure. The ASCOGONIUM (E, *ac*) is surrounded by an investment of cells, and has above it two cells, the uppermost of which becomes a projecting TRICHOGYNE and serves as the receptive organ for the spermatia. After fertilisation the ascogonium divides into three cells; the uppermost disappears, the lowest (F, *st*) remains sterile, while the asci grow out from the middle cell. Each ascus (G) contains four bicellular spindle-shaped spores.

Phylogenetically the Laboulbeniaceae are regarded by many authors as reduced Florideae on account of their possessing a trichogyne and spermatia. They exhibit no close relationship with the other orders of Ascomycetes.

Survey of the Ascomycetes. The ascus, with eight spores, less commonly with four or two spores, is characteristic of all Ascomycetes.

In the Sub-Class of the Protoascomycetes the ascus arises as the direct product of the fusion of the gametangia. The sexual process in the Euascomycetes, on the other hand, leads at first to the formation of ascogenous hyphae on which later the asci arise. In typical cases there is fusion between a multinucleate ascogonium, provided with a trichogyne and a multinucleate antheridium, so that there is a conjugation of gametangia; free spermatia are only rarely formed. The fusion of male and female nuclei does not take place in the ascogonium, but they pass, associated in pairs, into the ascogenous hyphae where they increase in number by conjugate division; the nuclear fusion is effected, after the stage of hook-formation, in the young ascus. Here also (as was the case for the Protoascomycetes) the reduction-division of the diploid fusion-nucleus takes place, so that the ascospores are haploid.

The life-history, considered from the point of view of an ALTERNATION OF GENERATIONS, may be divided in the following way. The GAMETOPHYTE is represented by the haploid mycelium bearing the antheridia and ascogonia. From the fertilised ascogonium the dikaryotic SPOROPHYTE with paired nuclei is developed in the form of the ascogenous hyphae. It ends with the formation of asexual haploid spores (the ascospores) which are developed in a sporangium (the ascus). The plectenchyma of the fructification is formed from the haploid gametophytic mycelium.

The phylogenetic position of the Ascomycetes is still a disputed question. There are two main opposed views regarding it.

According to one view, the Ascomycetes are regarded as derived from the Red Algae on account of the great resemblance of the sexual organs of some forms with those of this group of Algae. On this view Ascomycetes with relatively simple sexual processes must be regarded as reduced and phylogenetically younger forms.

According to the second view, the forms with simple sexual organs (Protoascomycetes) are the most primitive Ascomycetes. From them, by further elaboration of the sexual organs, the production of ascogenous hyphae (which enable an increased number of individuals to be produced by one sexual act), and of various types of fructification, the various orders of the Euascomycetes have developed. This view is based on the great resemblance of the sexual process in the Endomycetaceae to that in higher Phycomycetes, so that the latter would be the progenitors of the Ascomycetes.

The Orders of the Euascomycetes are characterised by the following characters derived from the fructifications—apart from those of the sexual organs:

Plectascales: Perithecia, spherical, closed; asci without regular arrangement.
Erysiphales: Perithecia, spherical, closed; asci as a central group.
Pyrenomycetales: Perithecia with an opening at the tip, flask- or urn-shaped.
Discomycetales: Apothecia with an open hymenium, saucer-, disc- or cup-shaped.
Tuberales: Fructification tuberous, subterranean, penetrated by tracts or chambers with the asci.
Exoascales: Fructification wanting.
Laboulbeniales: Fructification bristle-shaped, the only order with spermatia.

Sub-Class 2.—Basidiomycetes (1, 51, 52, 76-86)

The BASIDIUM is the characteristic organ of the Basidiomycetes. It is a structure that abstricts spores, in almost every case four spores, by a process of budding from as many distinct points. The basidium is club-shaped and unicellular in the HOLOBASIDIOMYCETES (Fig. 410 *C*) and septate in the PHRAGMOBASIDIOMYCETES (Figs. 425, 434).

A. Holobasidiomycetes

To this group belong the majority of those plants which are commonly recognised as fungi in our woods and meadows.

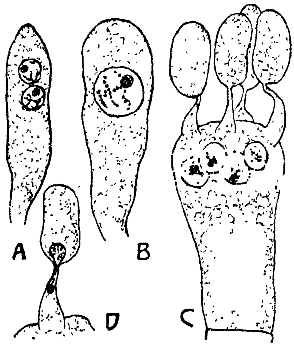


FIG. 410.—*Armillaria mellea*. *A*, Young basidium with the two primary nuclei; *B*, after fusion of the two nuclei. *Hypholoma appendiculatum*, *C*, a basidium before the four nuclei derived from the secondary nucleus of the basidium have passed into the four basidiospores. *D*, Passage of a nucleus through the sterigma into the basidiospore. (After RUHLAND.)

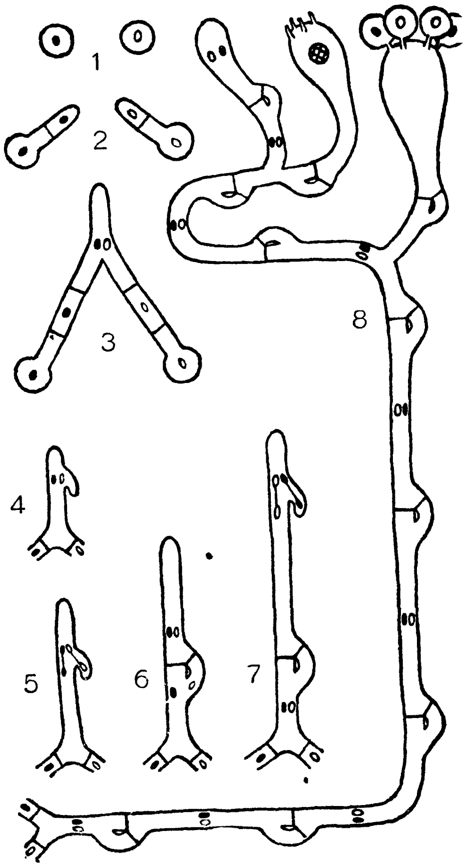


FIG. 411.—Diagrammatic scheme of a the development of Hymenomycete. *1*, Spores of different sex. *2*, Their germination to form a mycelium without clamp-connections. *3*, Conjugation. *4-6*, Formation of the first clamp-connection. *7*, Of the next. *8*. Mycelium with clamp-connections bearing a young binucleate basidium, a basidium with the fusion-nucleus, and a ripe basidium with two spores of each sex.

The course of the development is not the same in all representatives of the group, as is apparent especially from the investigations of KNIEP (76) (Fig. 411). The basidiospores are of different sexes. On their germination a mycelium with uninucleate cells, and of practically unlimited capacity of growth, is produced. No sexual organs are developed. But if the mycelium meets with a similar growth of another sex, fusions take place between vegetative cells of the two where they are in contact (Fig. 411, 3); the two sexual nuclei then lay themselves together without, however, fusing. A branch now arises from the fusion-cell and the pair of nuclei pass into this and undergo division in the following way. Just beside the pair of nuclei a hook-shaped lateral outgrowth arises from the cell; this is the beginning of what is known as a CLAMP-CONNECTION. One nucleus moves into the hook and divides, one of the resulting nuclei remaining in the hook, and the other passing back upwards into the cell. Meanwhile, the second nucleus has also divided, one of the resulting nuclei passes upwards towards the tip of the cell while the other remains in its basal part (Fig. 411, 5, Fig. 413). These two nuclei are now separated by a transverse wall which forms just beneath the clamp, and a second wall separates the cavity of the latter from that of the end cell. This terminal cell now contains a pair of nuclei that are sexually different. The lower cell also becomes binucleate since the nucleus in the hook enters it by an opening that forms at the tip of the hook, thus establishing the clamp-connection (Fig. 411, 6). The terminal cell continues to grow, and at each cell-division the clamp-connection is repeated; thus a branched mycelium, all the cells of which are binucleate and with a clamp-connection at every transverse wall, results (Fig. 411, 8). The mycelium can continue its growth for years in this condition, until under the influence of definite external conditions FRUCTIFICATIONS develop by the interweaving of hyphae. In the hymenial layer of the fructification the terminal cells of the hyphae enlarge and become converted into club-shaped BASIDIA (Figs. 412, 413). In these at last the two nuclei fuse; following on this comes the reduction-division which is connected with the determination of sex, and by the two successive divisions four haploid nuclei arise (Fig. 413). Meanwhile, the basidium has put out four thin, short outgrowths, the STERIGMATA (Fig.

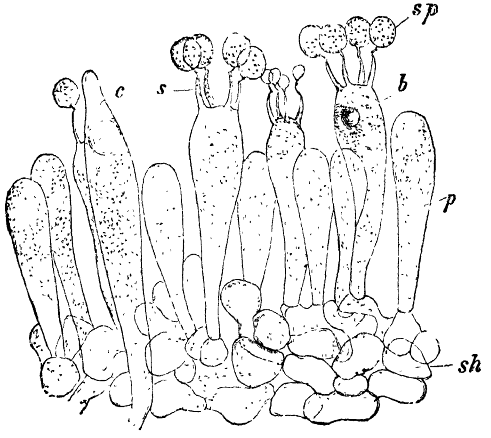


FIG. 412.—*Russula rubra*. Portion of the hymenium. *sh*, Sub-hymenial layer; *b*, basidia; *s*, sterigmata; *sp*, spores; *p*, paraphyses; *c*, a cystidium. (After STRASBURGER. × 540.)

410, *C*, *D*); one of the haploid nuclei passes into each of these and becomes the nucleus of the spherical or oval basidiospore (Fig. 412, *sp*) which arises from the end of the sterigma.

The four spores, of which two are of the one sex and two of the other, are projected for a short distance from the sterigmata by means of the turgor of the basidium (82). In addition to the basidia, the hymenium contains sterile hyphae with degenerated nuclear pairs, the paraphyses, and other sterile sacs, the cystidia (Fig. 412).

The origin of the phase with paired nuclei is usually not quite so simple as it has been described above. Further deviations from the normal type are met with, *e.g.* presence of more than two nuclei in the cells (Fig. 6), absence of clamp-connections, fructifications in the haploid stage, formation of only two spores on the basidium, etc. Some species are also of mixed sex and can give rise to a mycelium with paired nuclei without uniting with another mycelium (83).

The ALTERNATION OF GENERATIONS is not sharply marked. The haploid, sexually-differentiated mycelium which originates from the basidiospore corresponds to the gametophyte, but no longer bears sexual organs. The mycelium with paired nuclei, arising from it as a result of conjugation, represents the sporophyte. The basidium is homologous with a sporangium. The tissue of the fructification consists of hyphae with paired nuclei.

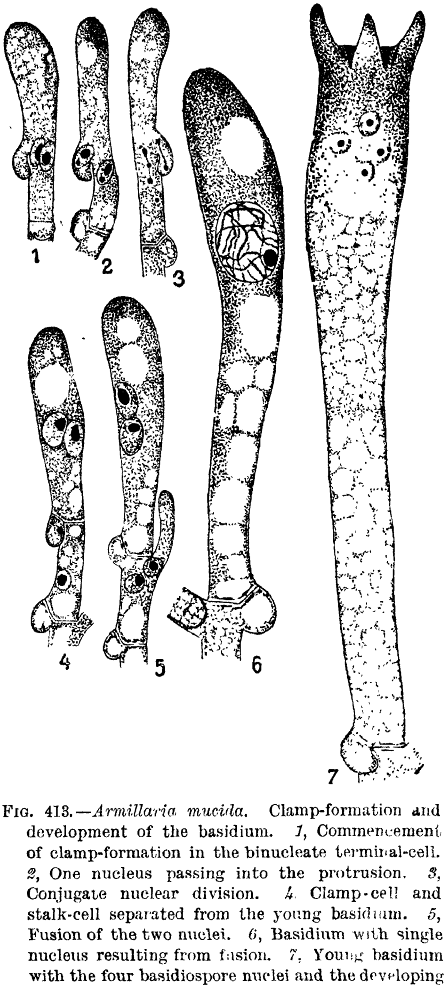


FIG. 413.—*Armillaria mucida.* Clamp-formation and development of the basidium. *1*, Commencement of clamp-formation in the binucleate terminal-cell. *2*, One nucleus passing into the protrusion. *3*, Conjugate nuclear division. *4*, Clamp-cell and stalk-cell separated from the young basidium. *5*, Fusion of the two nuclei. *6*, Basidium with single nucleus resulting from fusion. *7*, Young basidium with the four basidiospore nuclei and the developing sterigmata. (After H. KNIEP.)

Order 1. Hymenomycetales (70)

In the simplest Hymenomycetales the basidia are more or less isolated on the mycelium, while in the higher forms they are associated in a hymenium; the hymenial layers in turn come to be situated on a definite fructification, and in the mature condition are always freely exposed on the surface of the fructification.

Conidia, and more often oidia and gemmae, occur as accessory modes of reproduction, but play a much less important part than the basidiospores A ripe

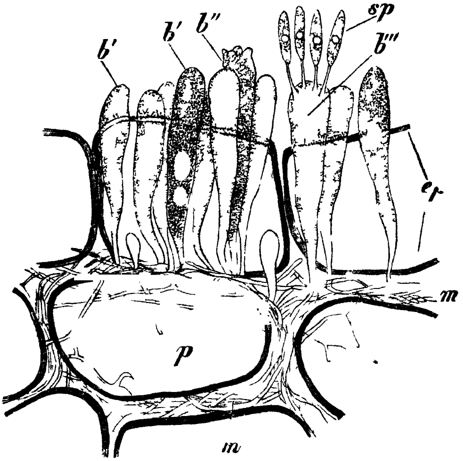


FIG 414 —*Exobasidium Vaccinii* Transverse section through the periphery of a stem of *Vaccinium* *ep* Epidermis *p*, cortical parenchyma *m*, mycelial hyphae *b* protruding basidia without sterigmat *b* , with young sterigmata *b″* with four spores (× 620 After WORONIN)

fructification of *Polyporus squamosus* sheds at least a million spores per minute The fructifications exhibit great variety of form

Thus *Corticium terrestre* has no fructification, but bears its basidia directly on

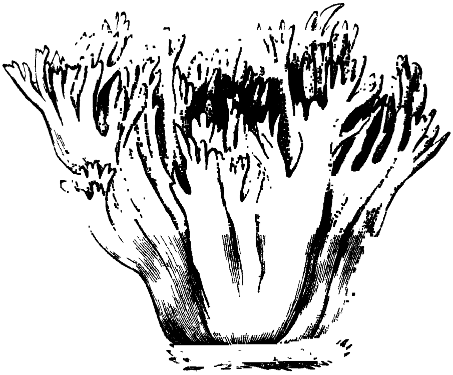


FIG 415 —*Clavaria botrytis* (Reduced After H SCHENCK)

the cobweb-like mycelium, which creeps over fallen twigs and moss Other representatives of the **Corticiaceae** form flat expansions or similarly simple hymenia. This is the case in *Stereum* which occurs commonly on tree-stumps, etc. *Exobasidium* (**Exobasidiaceae**), which is parasitic on species of *Vaccinium*, gives rise to red swellings of the parts of the plant affected ; its basidia are borne without any fructification beneath the epidermis, between the cells of which they project (Fig. 414).

In the club-shaped or coralloid fructifications of the **Clavariaceae** (Fig. 415) the whole surface is covered by the hymenium. In the family of the **Cantharellaceae**, to which the edible *Cantharellus cibarius* belongs, there is a distinction between portions with and without a hymenial layer ; the basidia are restricted to the ridged outer side of the top-shaped fructification.

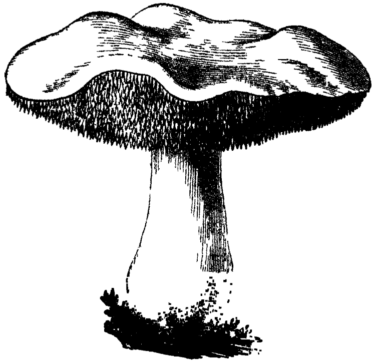


FIG. 416.—*Hydnum repandum.* (Reduced. After H. SCHENCK)

In the **Hydnaceae** the hymenium-bearing region takes the form of prickle-like outgrowths, which in the most advanced types cover the lower side of the stalked cap-shaped fructification (Fig. 416).

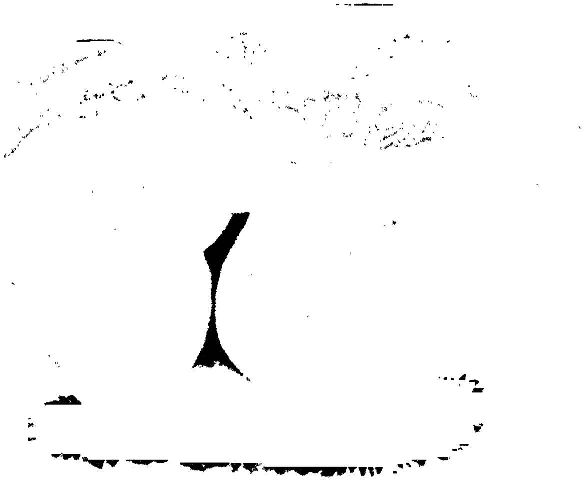


FIG 417.—*Boletus Satanas.* (After KROMBHOLZ, ½ nat. size.) *POISONOUS.*

In the Polyporeae in a wide sense the hymenial layer lines numerous tube-like canals which are placed vertically with regard to the general surface. Among the simplest of the fructifications are those of the **Meruliaceae** which are resupinate and have only shallow depressions ; *Merulius lacrymans* is the injurious Dry Rot Fungus and lives saprophytically in the wood of the joists, etc., of houses and destroys it. In addition to the growths of whitish-grey mycelium, this fungus forms firm mycelial strands in which there are vessel-like hyphae with wide lumina which serve to conduct water and food-materials ; thus from the originally infected moist region the fungus can extend into the dry parts of the house. The tubes are more defined in the fructifications of the **Polyporaceae** to which *Fomes fomentarius*, Touch-wood, belongs. Its mycelium lives as a parasite in deciduous trees, and forms large, bracket-shaped perennial fructifications. They have a hard, grey external surface, but inside are composed of softer, more loosely-woven hyphae, and were formerly used for tinder. The narrow tubes of the hymenium are disposed on the under side of the fructification in successive annual layers. *Polyporus officinalis*, which occurs on Larches in South Europe, is similarly formed and has an irregularly tuberous, white fructification; it contains a bitter, resinous substance. The various species of *Boletus* (Fam. **Boletaceae**) live saprophytically in the soil of woods. Their fleshy cap has a centrally placed stalk and bears the regularly formed tubes on its lower side. *Boletus edulis* and other species are edible; *Boletus satanas* (Fig. 417), on the other hand, is extremely poisonous. The stalk is yellow to reddish-purple and has red reticulate markings, while the pileus is yellowish brown on its upper surface, but on the under side is blood-red, changing later to orange-red. Some species of *Boletus* form mycorrhiza (p. 261).

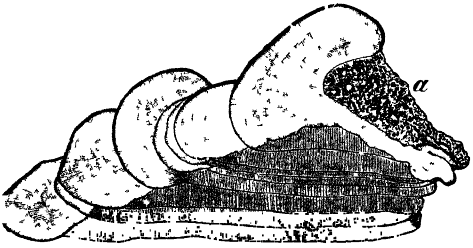


FIG. 418.—*Fomes igniarius*. Section through an old fructification, showing annual zones of growth. *a*, Point of attachment. (½ nat size. After H. SCHENCK.)

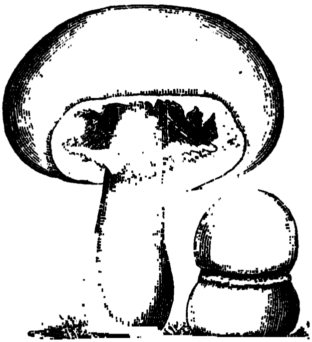


FIG. 419.—*Psalliota campestris*, Mushroom. To the right a young fructification. (Reduced.)

The Gill-Fungi or **Agaricaceae** include the largest number of species. The radially arranged lamellae or gills which are borne on the under side of the stalked cap or pileus are covered by the hymenium (Fig. 420). They mostly live as saprophytes in the soil of woods, but some are parasitic on trees. The fructifications in a young stage are roundish bodies, within which the stalk and cap are early differentiated. In many, a thin membrane (velum) extends from the margin of the cap to the stalk (Fig. 419); a similar structure is present in some species of *Boletus*. The velum ruptures later in development and may persist as a ring-shaped, attached, or movable structure (annulus) round the stalk; in some species it remains as a pendulous membrane on the upper part of the stalk (armilla). In *Amanita* (Figs. 420, 421) and related forms the young stalk and cap are enclosed by an envelope which remains as the volva at the base of the stalk and as white patches over the pileus.

The Mushroom (*Psalliota campestris*, Fig. 419) has a whitish cap and gills that are at first white, then pinkish, and ultimately blackish-brown; it occurs wild in fields but is also cultivated. There are other edible, though not artificially cultivated, Agarics, for example *Lactarius deliciosus*, characterised by an orange, milky juice, contained in specialised hyphae. Many cases of poisoning by fungi are caused by species of *Amanita*, which have the thick base of the stalk enclosed by a volva and white gills. *Amanita phalloides* (Fig. 421), with an olive-green cap, is the most poisonous. *A. mappa* is whitish-yellow with patches of the volva, and *A. verna* is white. *Armillaria mellea* is a dangerous parasite of trees; it contains a photogenic substance in its mycelium, which renders the infected wood phosphorescent (5).

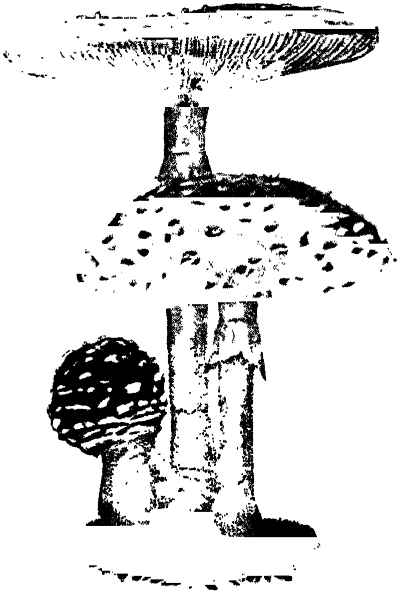


FIG. 420.—*Amanita muscaria.* (½ nat. size.) *POISONOUS.*

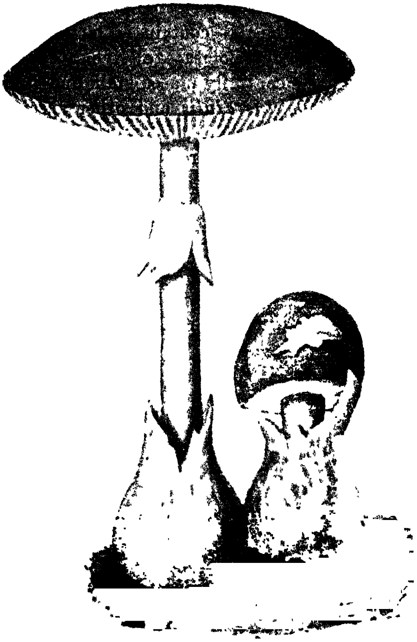


FIG. 421.—*Amanita phalloides.* (½ nat. size.) *VERY POISONOUS.*

Order 2. Gasteromycetales (70)

The Gasteromycetes are distinguished from the Hymenomycetes by their closed fructifications, which open only after the spores are ripe, by the rupture of the outer hyphal cortex or PERIDIUM. The spores are formed within the fructifications in an inner mass of tissue termed the GLEBA.

The Gasteromycetes are saprophytes, and develop their mycelium, which is from the beginning dikaryotic, in the humus soil of woods and meadows. Their fructifications, like those of the Hymenomycetes, are raised above the surface of the substratum, except in the group of the Hymenogastreae, which possesses subterranean, tuberous fructifications resembling those of the Tuberaceae.

The fructifications of *Scleroderma vulgare* (Fig. 422, 1) have a comparatively simple structure. They are nearly spherical, usually about 5 cm. thick, and have a thick, light brown, leathery peridium which finally becomes cracked and ruptured at the apex. The gleba is black when ripe, is traversed by numerous sterile veins, and is crowded with pear-shaped basidia which do not form a regular hymenium ; the basidia bear four sessile, spherical spores (Fig. 422, 2).

The genera *Bovista* and *Lycoperdon* (Fig. 423, 1) have also spherical fructifications, which are at first white and later of a brown colour. In the last-named genus they are also stalked, and in the case of *Lycoperdon Bovista* may even become half a metre in diameter. The peridium is formed of two layers ; the outer separates at maturity, while the inner dehisces at the summit. The hymenial layer of basidia, in the fungi of this group, lines the chambers of the gleba. The chambers are also provided with a fibrous capillitium consisting of brown, thick-walled, branched hyphae which aid in distributing the spores.

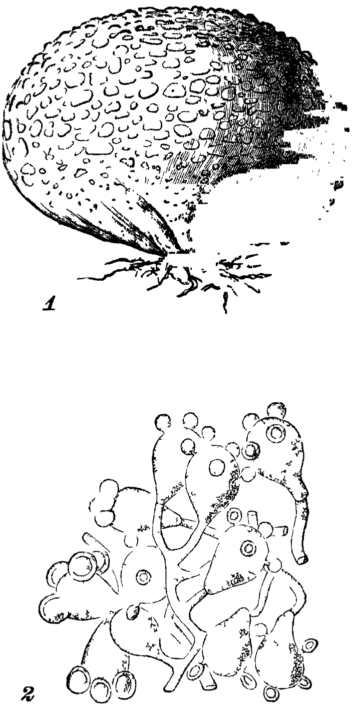


FIG. 422.—*1*, *Scleroderma vulgare*, fructification. *2*, Basidia of same. (After TULASNE.) (*1*, nat. size, *2*, enlarged.)

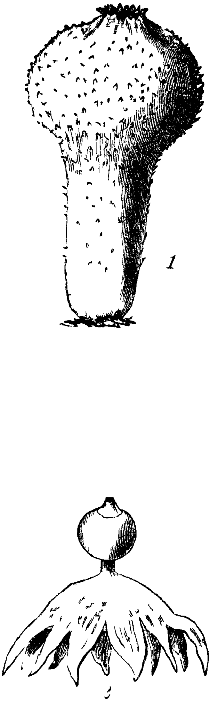


FIG. 423.—*1*, *Lycoperdon gemmatum*. *2*, *Geaster granulosus*. (Nat. size.)

In the related genus *Geaster* (Earth-star) (Fig. 423, 2) the peridia of the nearly spherical fructifications are also composed of two envelopes. When the dry fruit dehisces, the outer envelope splits into several stellate segments, and the inner layer of the peridium becomes perforated by an apical opening.

The highest development of the fructifications is exhibited by the **Phallaceae** (86), of which *Ithyphallus impudicus* (Stink-horn) is a well-known example. Its fructification recalls that of the discomycetous *Morchella*, but it has quite a different manner of development. A fructification of this species is about 15 cm. high. It has a thick, hollow stalk of a white colour and perforated with pores or chambers. Surmounting the stalk is a bell-shaped pileus covered with a brownish-green gleba which, when ripe, is converted into a slimy mass (Fig. 424). When young the fructification forms a white, egg-shaped body, and is wholly enveloped by a double-walled peridium with an intermediate gelatinous layer. Within the PERIDIUM, the hyphal tissue becomes differentiated into the axial stalk and the bell-shaped pileus, carrying the gleba in the form of a mass of hyphal tissue, which contains the chambers and basidial hymenium. At maturity the stalk becomes enormously elongated, and, pushing through the ruptured peridium, raises the pileus with the adhering gleba high above it. The gleba then deliquesces into a dropping, slimy mass, which emits a carrion-like stench serving to attract carrion-flies, by whose agency the spores embedded in it are disseminated.

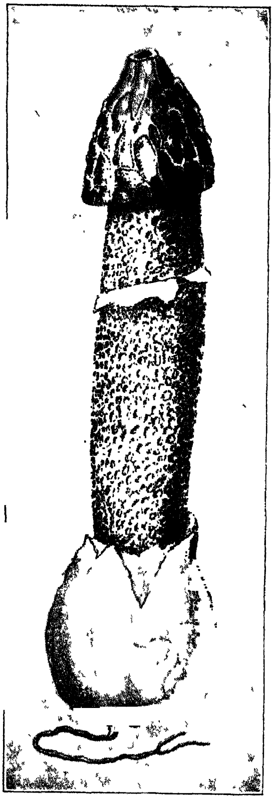


FIG. 424.—*Ithyphallus impudicus*. (½ nat. size.)

B. Phragmobasidiomycetes

The basidium is four-celled, being divided by longitudinal walls or more commonly by transverse walls; in a few exceptional cases it is unicellular.

Order 1. Tremellales (85)

The basidium is longitudinally divided and bears four spores (Fig. 425). There is an ascending series leading from forms without fructification to those with gelatinous fructifications which are covered on their upper surface by the hymenium. The few genera are saprophytic on rotting stems of trees.

Order 2. Auriculariales (85)

The Auriculariales also form a developmental series from primitive web-like forms without a hymenial layer to those with a differentiated fructification. Thus the Jew's ear fungus (*Auricularia sambucina*), which grows on old Elder stems, has gelatinous, dark-brown, shell-shaped fructifications which bear the hymenium on their inner side. The basidia of all the Auriculariales are divided by transverse walls into four cells lying in a row above one another; from each of these a sterigma is formed laterally and bears a spore (Fig. 426). In many forms the basidium has a swelling at its base known as a PRO-BASIDIUM (Fig. 426); this originally formed the end of a hypha with paired nuclei and the nuclear fusion occurred within it. Later the true septate basidium grows from the pro-basidium.

Order 3. Uredinales (Rust Fungi) ($^{78-81}$)

In this Order, which includes some 1000 species, the basidia are transversely septate and four-celled (Fig. 427, 2); they are thus very similar to those of the Auriculariales. The mycelium cannot be artificially cultivated; it lives parasitically in the intercellular spaces of the higher plants, most commonly in their leaves, and sends haustoria into the cells. These fungi cause widespread diseases that are spoken of as Rusts. No fructifications are formed, but the group is characterised by the variety in type of the spores which appear in a strict order of succession (Fig. 433). The typical course of development is as follows (^{78}).

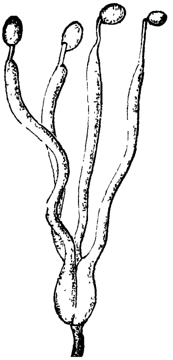


FIG. 425.—Basidium of *Tremella lutescens*. (After BREFELD.) (× 450. From v. TAVEL, *Pilze*.)

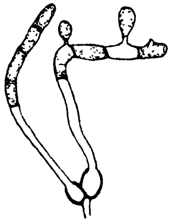


FIG. 426.—*Sacoblastia ovispora*. Two transversely septate basidia with pro-basidia at their bases; that on the right shows the commencement of spore-formation.

The basidiospores germinate in the spring on the leaves of a host-plant and give rise to a mycelium with uninucleate cells which grows in the intercellular spaces. On this mycelium two kinds of spores are later produced; these are the small "spermatia," which are formed in spermogonia, and are incapable of further development, and the larger aecidiospores, formed in aecidia and capable of infecting a host-plant.

The SPERMOGONIA are flask-shaped structures which break through the epidermis of the upper side of the leaf (Fig. 428), and abstrict small, uninucleate elliptical cells, the "SPERMATIA" from the hyphae lining the basal region. These spores may produce a short germ-tube in nutrient solutions, but are not capable of infecting a host-plant. They have no importance for the development of the fungus and are wanting in many species.

The AECIDIA break through the epidermis of the under side of the same leaves, They are cup-shaped structures (Fig. 429) filled with parallel chains of AECIDIOSPORES. Their development commences, in the case of *Phragmidium speciosum*, parasitic on Roses, with a palisade-like arrangement of uninucleate hyphae beneath the epidermis (Fig. 430 A). The end of each hypha divides into an upper sterile cell, which soon degenerates, and a larger, lower fertile cell (B). Between every two neighbouring fertile cells the walls are broken down in the upper part so that they fuse in pairs (C); their nuclei do not, however, fuse, but become placed side by side. From then on the pair of nuclei divide conjugately, the

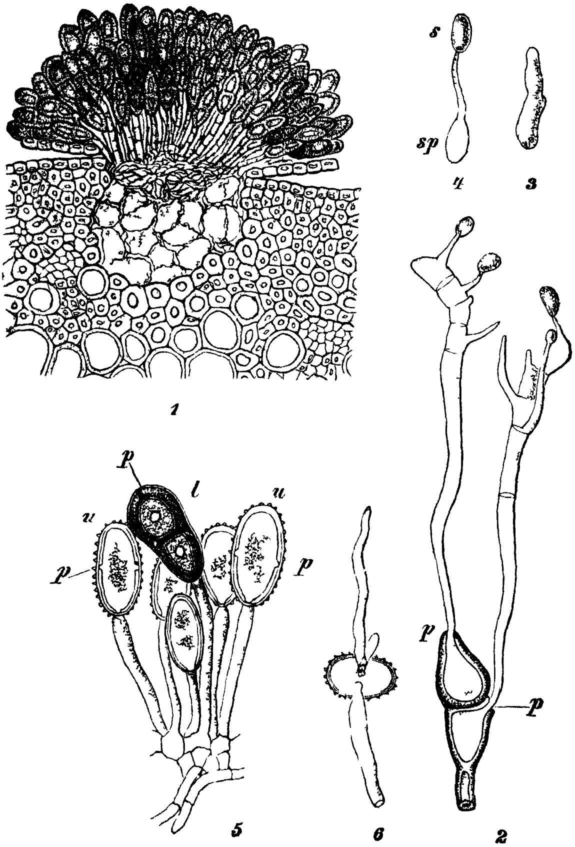


Fig. 427.—*Puccinia graminis.* 1, Transverse section through a grass haulm with group of teleutospores. 2, Germinating teleutospore with two basidia. 3, 4, Germinating basidiospores; the latter has formed a secondary spore not having been able to infect a host-plant. 5, A portion of a group of uredospores (*u*) and teleutospores (*t*); *p* the germ pores. 6, Germinating uredospore. 1, 2, 3, 4 after Tulasne; 6 after De Bary. 1 × 150, 2 × circa 230, 3, 4 × 370, 5 × 300, 6 × 390. (From v. Tavel, *Pilze*.)

one resulting pair of nuclei passing towards the tip of the cell and the other pair remaining in its basal part; between the two pairs a transverse wall is formed (D, E). This process is repeated many times in the basal cell so that a chain of binucleate cells (AECIDIOSPORE MOTHER CELLS) is formed. Each spore mother cell divides once, with conjugate division of its pair of nuclei, into an upper, larger cell, which is the binucleate AECIDIOSPORE and a lower binucleate small cell, which is the INTERCALARY CELL (F). The latter become mucilaginous and disappear, setting the aecidiospores free (G) In some genera (*e g. Puccinia*) the uppermost spores of the rows and all the spores of the peripheral rows lose their spore-like characters and cohere to form a firm investment (PERIDIUM, Fig. 429). Owing to the pressure caused by the continued new formation of spores at the lower ends of the chains (in *Puccinia graminis* over 10,000 spores are formed in an aecidium), the epidermis is ruptured and the rust-coloured spores are set free and can be distributed by the wind.

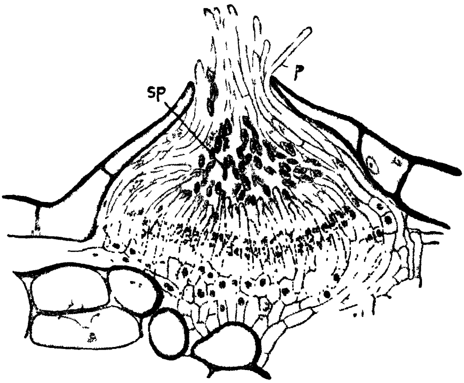


FIG. 428 —*Gymnosporangium clavariaeforme* A spermogonium rupturing the epidermis of a leaf of *Crataegus*, *sp*, spermatia, *p*, sterile paraphyses. (After BLACKMAN)

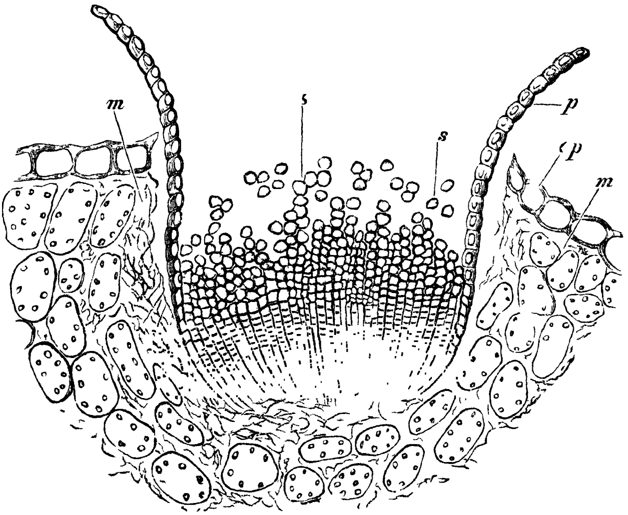


FIG. 429 —*Puccinia graminis* Aecidium on *Berberis vulgaris* *ep* epidermis of lower surface of leaf, *m*, intercellular mycelium, *p*, peridium, *s*, chains of spores (× 142)

They germinate on a new host plant The germ tube enters by means of a stoma and develops to an intercellular mycelium with binucleate cells which soon proceeds to form UREDOSPORES or summer spores These arise singly by the enlargement of the terminal cell of the hypha which forms the stalk, and are associated in roundish or linear sori, which break through the epidermis of the host plant as rusty patches Each uredospore contains a pair of nuclei which, like those of the mycelium, have arisen by conjugate division (Fig 431). The uredospores spread the fungus during the summer Later in the year differently constructed spores, the TELEUTOSPORES, or winter spores, are formed in the same (Fig 427, 5), or in other (Fig 427, 1) sori These are thick walled, usually more darkly coloured, and unicellular (*Uromyces*), bicellular (*Puccinia*, Fig 427),

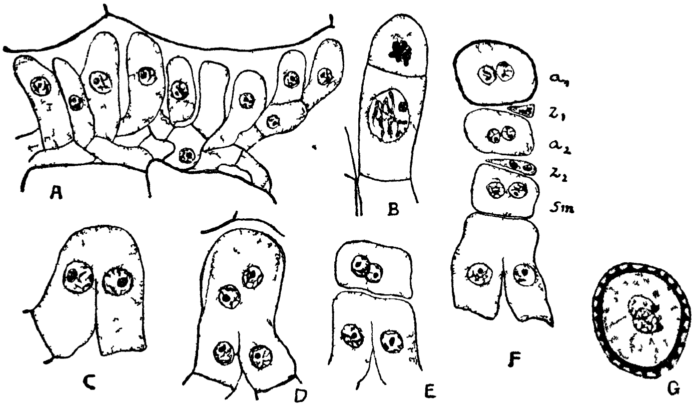


FIG 430 —*Phragmidium speciosum* *A* The first rudiment of an aecidium beneath the epidermis of a leaf of *Rosa* *B* The division of the end cell of a hypha into the upper transitory sterile cell and the lower fertile cell *C* Conjugation of two adjoining fertile cells *D* Later stage in which the first nuclear division is completed *E* Abstriction of the first aecidiospore mother cell *F* Chain of aecidiospores (a_1 a_2) separated by intercalary cells (z_1 z_2) *sm* the last formed spore mother cell still undivided (After CHRISTMAN) *G* Ripe aecidiospore of *Phragmidium violaceum* (After BLACKMAN)

or multicellular (*Phragmidium*, Fig 432) When young they are binucleate but as they mature THE PAIRED NUCLEI THEY CONTAIN FUSE (Figs 432, 433). Each teleutospore corresponds to the EARLY STAGE OF A BASIDIUM which, however (since the thick walled teleutospore forms a resting structure over the winter), does not at once develop further, but germinates in the ensuing spring to form a tubular BASIDIUM (427, 2) The teleutospore thus corresponds to the pro basidium of the Auriculariales (cf Fig 426 The four haploid nuclei which arise by division of the fusion nucleus, are separated by transverse walls (Fig 433, 7) From each of these cells a sterigma grows, and ends in the haploid BASIDIOSPORE (Fig 427, 2) The basidiospores are forcibly thrown off from the sterigmata They are carried by the wind to the leaves of the host plant and this completes the developmental cycle (Fig 433)

All Uredineae do not exhibit so complicated a course of development (^{79}), since in many cases one or more of the five forms of spores are omitted Thus in the fungus which causes the Rust disease of Malvaceae, *Puccinia malvacearum*, there are no spermogonia, aecidia, or uredospores, the binucleate condition is attained by the fusion of two cells in the young teleuto sorus Teleutospores are almost always present in the life-history. They are absent in very few species (81, 81a), for example, in *Endophyllum sempervivi*; in this the basidia develop from the aecidiospores in which the nuclear fusion, which usually occurs in the teleutospores, takes place.

Some Rust-Fungi go through their whole life-history on the same kind of host-plant; these are termed AUTOECIOUS. In the HETEROECIOUS Uredineae, on the other hand, the haploid phase (the haplont) and the binucleate phase (the dikaryont) develop on different kinds of host-plant.

An example of such an alternation of hosts is afforded by *Puccinia graminis* (80) (Fig. 427), the commonest of the Rusts of Wheat. Its basidiospores will only germinate on the leaves of the Barberry (and the young fruits of *Mahonia aquilegifolia*) and produce on this host-plant the spermogonia and the aecidia. The basidiospores, on the other hand, will only germinate on the Gramineae, producing on them the uredospores and teleutospores in rusty-brown or blackish linear sori. Similarly in *Uromyces pisi* the spermogonia and aecidia occur on *Euphorbia cyparissias* and *E. esula*, and the uredo- and teleuto-spores on *Pisum sativum*, *Lathyrus pratensis* and *L. sylvestris*. The infected plants of *Euphorbia* remain unbranched, have yellowish, abnormally short and thick leaves, and do not, as a rule, flower. These forms of Rust are thus very selective as regards their hosts; there are, however, heteroecious species, the haplonts or dikaryonts of which can grow on many different host-plants (79).

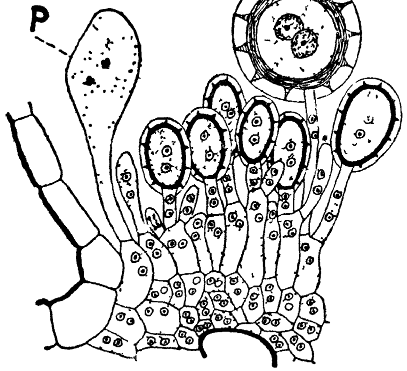


FIG. 431.—*Phragmidium rubi*. Marginal portion of an almost mature uredo-sorus after it has broken through the epidermis. The mycelium and the uredospores have paired nuclei. P. paraphysis. (After GAUMANN × 565.)

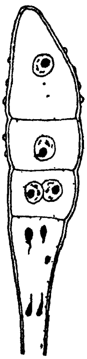


FIG. 432.—*Phragmidium violaceum*. Teleutospore. The lower cell has a pair of nuclei; these have fused in the two upper cells. (After BLACKMAN from GAUMANN. × 700)

The Rust-fungi, although they do not kill the tissues of the host-plants, give rise to serious diseases of plants. Thus in forestry the aecidium generation of *Melampsora caryophyllacearum* causes witches'-brooms, and canker of Abies, while its uredo- and teleuto-spores occur on Caryophyllaceae. *Cronartium ascelepiadeum* is still more injurious since its aecidial stage attacks and kills the branches of pines. *Puccinia graminis* causes great harm, especially to winter wheat, weakening the plants and diminishing the yield. The attempt to eradicate the disease by destroying all Barberry plants does not succeed, since the uredospores can live over the winter and then infect the young wheat-plants. No chemical remedies are known.

The typical Uredineae show a clear alternation of nuclear phases and a corresponding ALTERNATION OF GENERATIONS.

The HAPLOID GAMETOPHYTE develops from the haploid basidiospore; it ends with the cell-fusion that takes place in the young aecidium and represents a reduced sexual process. The binucleate aecidiospore-mother-cells represent the beginning of the DIKARYOTIC SPOROPHYTE; this has the uredospores as a subsidiary form of reproduction and ends with the basidia in which the reduction-division takes place. The teleutospores are not for the spread of the plant, but are to be regarded as the young basidia modified for persistence through the winter. The gametophyte and sporophyte in some cases differ in their nutritive physiology and grow on different host-plants.

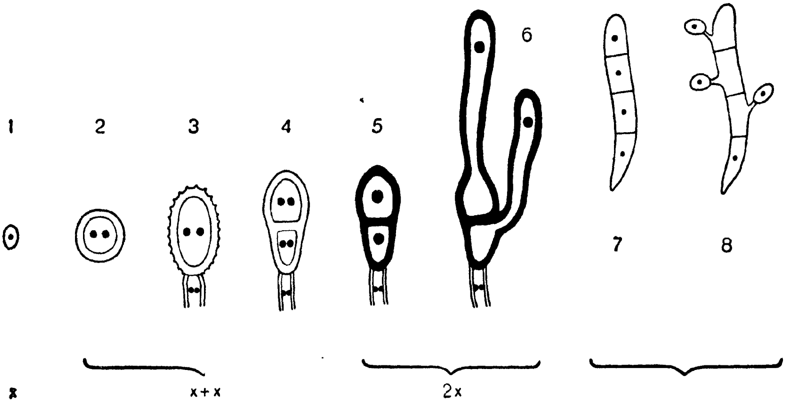


FIG. 433.—Diagrammatic representation of the succession of spores in *Puccinia graminis* 1, basidiospore; 2, aecidiospore (on *Berberis*); 3, 4, 5, uredospores and teutospores (on wheat); 6, 7, 8, development of the basidium.

There is still difference of opinion regarding the nature of the "spermatia." As the name indicates they are often regarded, with BLACKMAN, as male gametes that have become functionless. They may, however, be alternatively regarded as conidia which have become functionless, and the structures in which they arise would then be termed pycnidia, instead of spermogonia.

Order 4. Ustilaginales (Smut Fungi) (77)

The Ustilagineae, which form no fructifications, live as parasites in the intercellular spaces of higher plants, but can be grown in culture. In typical cases their development is as follows:

The brand-spores (resting spores) which are distributed by the wind in autumn retain the power of germination for years; in spring they germinate, forming a basidium which abstricts BASIDIOSPORES (Fig. 434). The latter are sexually differentiated and conjugate on germinating or shortly afterwards (Fig. 437 A), giving rise to a dikaryotic mycelium which at first is saprophytic. This mycelium infects the host-plant and, at least in the case of some species, is extensively developed as a mycelium with clamp-connections. At certain spots, e.g. in the ovaries of cereals, the mycelium forms denser masses and its cells swell in bead-like rows (Fig. 435), and become isolated as thick-walled dark spores. These BRAND-SPORES are shed from the place of their formation like a black dust. When young, each spore has two nuclei, but as the spore matures these fuse; on the formation of the basidium, reduction-division, associated with the sex-determination, occurs. The basidiospores are thus haploid and sexually distinct. The brand-spores are evidently homologous with the teleutospores of the Uredineae.

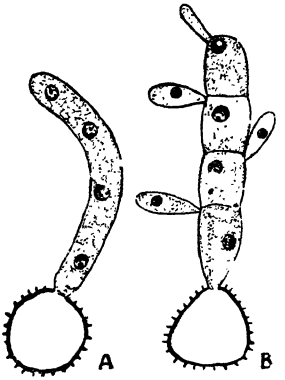


FIG. 434.—*Ustilago scabiosae.* *A*, Young basidium with four nuclei formed on germination of the resting spore. *B*, Spore-formation on the 4-celled basidium. (After HARPER.)

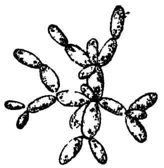


FIG. 436. — *Ustilago.* Basidiospore in nutrient solution, undergoing yeast-like budding. (After BREFELD, from VON TAVEL, *Pilze.* (× 350.)

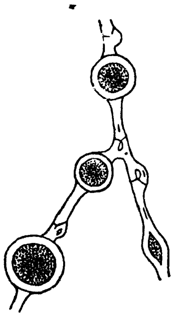


FIG. 435.—*Ustilago Veijichii.* Formation of brand-spores from a mycelium with clamp-connections. (After SEYFERT.)

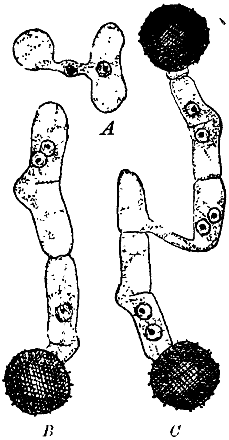


FIG. 437.—*Ustilago carbo.* *A*, conjugating sporidia. *B*, The two uppermost cells of a basidium united to form a cell with paired nuclei. *C*, conjugation between two basidia. (After RAWITSCHER. × 1000.)

Considerable differences in detail are found between the two families of the Ustilaginaceae and Tilletiaceae, and between their individual species.

In the **Ustilaginaceae** the brand-spore, which has rested during the winter, puts out a germ-tube (Fig. 434 *A*) into which the diploid nucleus passes and undergoes division into four haploid nuclei; transverse walls form between these nuclei, and a BASIDIUM, resembling those of the Auriculariaceae and the Uredineae, results (Fig. 434). This structure, which is also spoken of as a PROMYCELIUM, now abstricts from the side of each cell a BASIDIOSPORE (sometimes termed a SPORIDIUM); in this process the nucleus does not itself pass from the basidium into the spore, but divides, and a daughter-nucleus enters the spore (Fig. 434 *B*). Under favourable nutritive conditions it is therefore possible for further basidiospores to be abstricted. The basidiospore may grow into a filamentous mycelium, but more frequently forms chains of yeast-like cells (Fig. 436). Mycelia or the isolated cells of the chains, when of different sex, then conjugate with one another. The basidiospores themselves may unite, or an association of the sexually different nuclei of the basidium may take place (Fig. 437 *B*), or two basidia may be united by a conjugation tube (Fig. 437 *C*).

In the **Tilletiaceae** transverse walls are not present in the basidium. The elongated basidiospores are borne, to the number of four or eight, at the summit of the basidium (Fig. 438 *A*) and conjugate in pairs while still attached. Either they are shed thus connected in pairs (*Tilletia tritici*, Fig. 438 *B*) and germinate to form a mycelium with paired nuclei; or the growth of the dikaryont takes place without separation of the spores from the basidium (*Urocystis violae*, Fig. 438) so that the mycelium with paired nuclei seems to arise directly from the brand-spore (Fig 438 *F*). In *Tilletia tritici* the dikaryotic stage can reproduce by means of conidia.

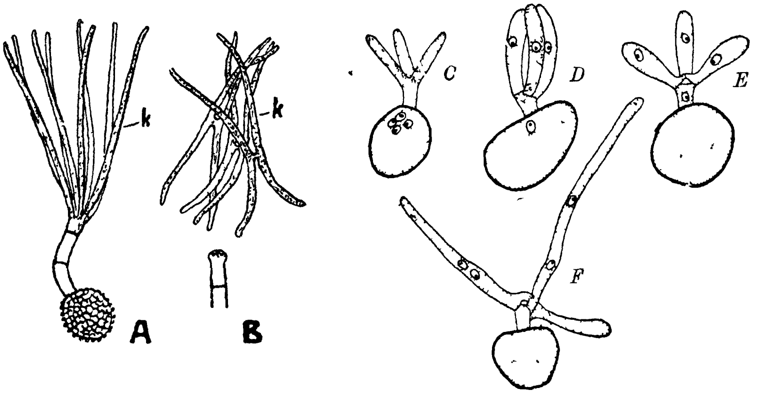


FIG. 438.—*Tilletia tritici*. *A*, The basidium developed from the brand-spore bearing at the end four pairs of spores *k* (× 300). *B*, The dispersion of the spores which have fused in pairs (× 250). (After BREFELD.) *Urocystis vulgare*, *C*, Brand-spores with the four basidiospore nuclei. *D*, basidium with three uninucleate basidiospores at its tip. *E*, Conjugation of two basidiospores. *F*, Growth of the mycelium with paired nuclei. (After KNIEP, from GAUMANN. × 450.)

One of the most remarkable structural changes induced by disease-producing fungi results from the presence of *Ustilago violacea* in the female flowers of species of *Melandryum*; in these stamens develop, the anthers being filled with brand-spores in place of pollen.

The smut-diseases of cereals are of great agricultural importance. *Ustilago zeae* produces abscess-like swellings, filled with brand-spores, on the stems, leaves and inflorescences of the maize. *Ustilago avenae*, *U hordei* and *U. tritici* fill the ovaries of Oats, Barley, and Wheat with a dusty mass of brand-spores. Species of *Tilletia* form compact masses of spores, with a smell of herrings, in the grains of Wheat (and occasionally also in those of Rye and Barley; the so-called STINK-BRAND. Since one affected grain of Wheat contains four to twelve million spores, which on threshing are dusted over the seed, the disease is readily spread to many seedlings of the next sowing. As a result there is often a loss of 20 per cent and sometimes of 60 per cent of the harvest. The smut-diseases are successfully treated by a short immersion of the seed in poisonous solutions of salts of mercury, etc., by which the brand-spores are killed.

Survey of the Basidiomycetes.—The Basidiomycetes exhibit clear phylogenetic connections with the Ascomycetes.

As in the latter group the fusion of the sexual cells (PLASMOGAMY) is separated from the fusion of the sexual nuclei (KARYOGAMY) by the characteristic STAGE WITH PAIRED NUCLEI (dikaryont) The formation of CLAMP-CONNECTIONS on the mycelium with paired nuclei in the Basidiomycetes is homologous with the HOOK-FORMATION of the Ascomycetes. In the latter this is limited to the terminal cells of the ascogenous hyphae (in rare cases it takes place in other cells) while in the Basidiomycetes clamp-connections appear at all the divisions. In both groups the FUSION OF THE PAIRED NUCLEI only occurs in the terminal cells of the dikaryont, and is followed immediately by the REDUCTION-DIVISION and the formation of the haploid ASCOSPORES and BASIDIOSPORES respectively. The BASIDIUM is therefore homologous with the ASCUS and only differs by the exogenous production of the spores.

The absence of sexual organs in the Basidiomycetes, in contrast to their occurrence in Ascomycetes, does not prevent the assumption of a relationship, for in many of the higher Ascomycetes the sexual organs are reduced. Since the holobasidium is most like the ascus the simplest Hymenomycetales are regarded as standing closest to the lower Ascomycetes ; the Phragmobasidiomycetes are regarded as derived from the Hymenomycetes, the Ustilagineae and Uredineae in which fructifications are lacking being reduced terminal groups. Other views are, of course, possible ; if the spermatia of the Uredineae are assumed to be male gametes this group may form a connection with correspondingly organised Ascomycetes.

Economic Uses.—*Polyporus fomentarius* (FUNGUS CHIRURGORUM). *Polyporus officinalis* (=*Boletus laricis*) gives AGARICUS ALBUS, AGARICINUM, and ACIDUM AGARICINUM.

Short Survey of the Orders of the Basidiomycetes.

Hymenomycetales: Basidia non-septate. Fructification with hymenium exposed.
Gasteromycetales : Basidia non-septate. Fructification closed.
Tremellales : Basidia longitudinally divided. Fructification gelatinous.
Auriculariales : Basidia transversely divided. Fructification gelatinous.
Uredinales : Basidia transversely divided. Fructification wanting. Characteristic succession of spermatia, aecidiospores, uredospores, and teleutospores.
Ustilaginales : Basidia transversely divided or undivided. Fructification wanting. Characteristic spore-form (brand-spores).

Fungi Imperfecti.—In the case of many fungi neither asci nor basidia, but only conidia, are so far known. These are therefore classed as Fungi Imperfecti, leaving open the question whether or not in particular cases the power of forming asci or basidia has become completely lost.

Fungi are only poorly preserved in the fossil condition. The oldest known are from rocks of Middle Old Red Sandstone Age.

CLASS XIII

Lichenes (Lichens) (1, 51, 87 91)

If a section is made of the thallus of any Lichen, a mixture of fungal hyphae and algae can always be demonstrated (Fig. 439). The lichen thallus is thus a consortium.

The Algae occurring in Lichens are sometimes unicellular (*e.g. Chroococcus*), or filamentous (*e.g. Nostoc*) Cyanophyceae. Frequently they belong to the Green Algae ; they are often unicellular Protococcaceae (*e.g. Cystococcus humicola*), or may be filamentous Ulotrichales (*e.g. Stichococcus*, *Trentepohlia umbrina*). The fungi concerned are mostly Ascomycetes (Discomycetes and less commonly Pyrenomycetes), and only in a very few cases Basidiomycetes. Both the fungus and the alga can, as a rule, be artificially cultivated apart from one another.

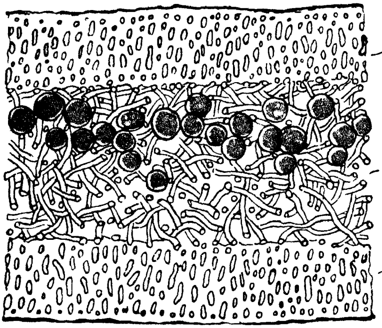


FIG. 439.—*Cetraria islandica.* Transverse section through the thallus; *or*, cortical layer of upper surface; *ur*, of the lower surface; *m*, medullary layer containing the green cells of the Alga *Cystococcus humicola.* (× 272. After H. SCHENCK.)

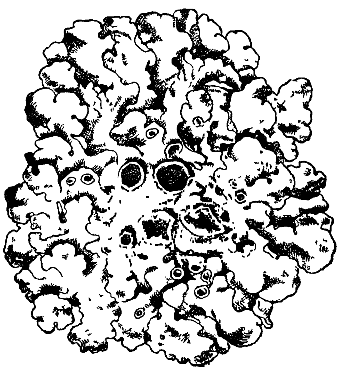


FIG. 440. *Parmelia acetabulum*; grows on trees. (After REINKE.)

In the simplest cases the fungus grows in the mucilaginous walls of the alga ; thus in *Collema*, which is common on soil and bark, the mycelium is present in the mucilage of a *Nostoc*-colony. Such Lichens, which are swollen when moist and contract to a thin layer when dry, are termed GELATINOUS Lichens. In other cases the fungal hyphae are spun around the individual filaments of the alga in a thin layer (*e.g.* in *Ephebe pubescens*) ; what is termed a FILAMENTOUS thallus results from this. In both these types the external form of the lichen is determined by that of the alga. Such lichens are termed HOMOIOMEROUS in contrast to HETEROMEROUS forms, in which the fungal and algal constituents of the Lichen appear stratified and the external shape is determined by the fungus. The majority of Lichens have this type of thallus. The internal portion of the thallus usually consists of loosely arranged hyphae, among which the algal cells form groups or a definite layer usually lying near the upper surface ; the external layers of the thallus are frequently formed of a dense cortex composed of a plectenchyma of interwoven hyphae (Fig. 439).

It is customary to distinguish the three following forms of heteromerous Lichens :—CRUSTACEOUS LICHENS, in which the thallus has the form of an incrustation adhering closely to a substratum of rocks, bark, or to the soil, which the hyphae to a certain extent penetrate. FOLIACEOUS LICHENS (Fig. 440), whose flattened, leaf-like, lobed, or deeply cleft thallus is attached more loosely to the substratum by means of rhizoid-like hyphae (rhizines), springing either from the middle only or irregularly from the whole under surface. FRUTICOSE LICHENS (Figs. 441, 442) have a filamentous or ribbon like thallus branched in a shrub-like manner and attached at the base.

The growth of the thallus in Lichens is as a rule very slow. The exceptionally quick-growing *Cetraria islandica* (Fig. 445) may form several centimetres of new growth in a year ; usually less than a centimetre is formed. Under good conditions of illumination *Parmelia furfuracea* attains in ten years a diameter of only 31 × 60 mm. (88a). The fructifications do not form as a rule until the plant is some years old.

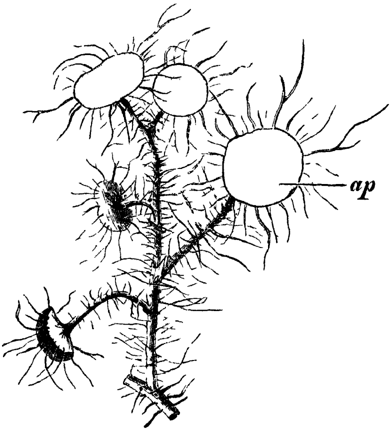


FIG. 441.—*Usnea barbata.* *ap*, Apothecium. (Nat. size. After H SCHENCK.)

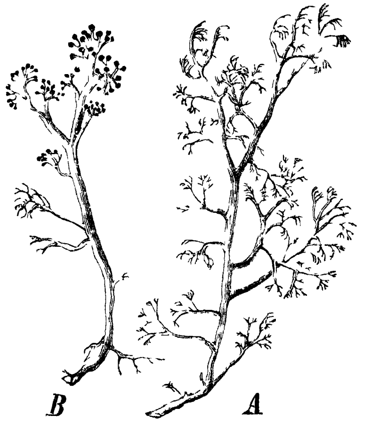


FIG. 442 – *Cladonia rangiferina.* *A*, sterile , *B*, with ascus-fruits at the ends of the branches. (Nat. size. After H. SCHENCK.)

Many Lichens are able to multiply in a purely vegetative manner, by means of loosened pieces of the thallus, which continue their growth and attach themselves to the substratum with new rhizines. The majority of the heteromerous lichens possess in the formation of SOREDIA another means of vegetative multiplication. In this process, small groups of dividing algal cells become closely entwined with mycelial hyphae and form small isolated bodies which, on the rupture of the thallus, are scattered in great numbers by the wind and give rise to new lichens. Frequently the soredia arise in circumscribed receptacles (soralia) (Figs. 443, 444).

The fructifications of the Lichens are produced by the fungi, not by the algae, which are always purely vegetative.

In their natural habitats the lichen-fungi only develop from their spores when the appropriate algae are available.

Only in a few genera (*e.g. Endocarpon*) are special small algal cells present in the fructification; they are shed along with the spores, and are enveloped by the germ-tubes developed by the latter.

The fungus and alga are symbiotically associated in the lichen thallus.

The fungus derives its nourishment from the organic matter produced by the assimilating alga; it can also, though rarely, send haustoria into the algal cells (Fig. 448), and so exhaust their contents and also live saprophytically on the dead algal cells. The alga, on the contrary, derives a definite advantage from its consortism with the fungus, receiving from it inorganic substances and water, and probably organic substances also. The main advantage in this mutualistic symbiosis is probably on the side of the fungus. This is especially the case in those Lichens which grow on bare rock.

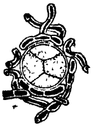


FIG. 443.—*Parmelia physodes*, soredium. (After NIENBURG.)

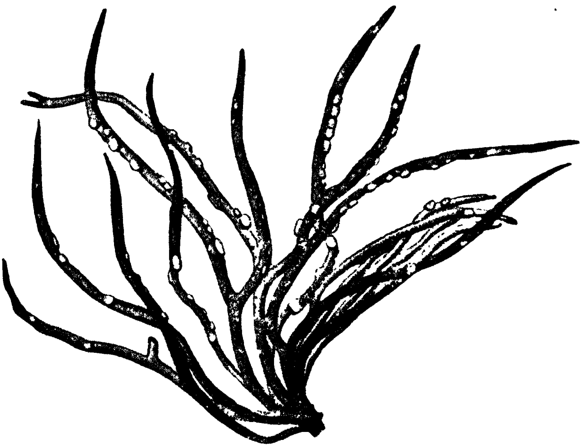


FIG. 444.—*Roccella tinctoria*, DC. Canary Islands. With marginal soralia. (After WIESNER.)

The supply of water (^{87a}) in Lichens is obtained by means of the alga in the case of gelatinous lichens. In the heteromerous forms it is the fungus which performs this function. As a rule this is effected by thick-walled hyphae which are readily wetted by water and absorb it by their swelling walls; the cortex is composed of such hyphae and strands of them may also be present within the thallus. The hyphae in the neighbourhood of the algal cells, on the other hand, are not wetted by water, so that, even in moist weather, the access of air to the alga is not interfered with. Further the openings in the cortex found in some lichen thalli (so called breathing pores) which serve for ventilation are, in contrast to the general surface of the cortex, not wetted. This property of not being wetted results from the presence of lichen acids (^{88}) excreted in the form of crystals on the surface of the hyphae; they are organic acids the origin of which depends on the chemical interaction of the alga and fungus. Lichens can endure drying for months without injury and can also obtain water hygroscopically from moist air.

1. Ascolichenes

Only a few genera of Lichens have flask-shaped perithecia, the fungus belonging to the Pyrenomycetes (*Endocarpon, Verrucaria*). Most genera produce, as the ascus-fruit of their fungus, cupular or discoid apothecia, sessile or somewhat sunk in the thallus and belong to the Discomycetes (Figs. 441, 445).

One of the commonest species of fruticose lichens belonging to this group is *Usnea barbata*, the Beard Lichen, frequently occurring on trees and having large fringed apothecia (Fig. 441). *Ramalina fraxinea*, which has a broad ribbon-shaped branched thallus and grows on trees, and the numerous species of *Roccella* (Fig. 444) found on the rocks of warmer coasts, have similar apothecia. *Cetraria islandica*, Iceland Moss (Fig. 445), occupies an intermediate position between the fruticose and foliaceous lichens. It has a divided, foliaceous, but partially erect thallus, which is of a light bluish-green or brown colour, whitish on the under side, and bears the apothecia on its margin. This Lichen is found in mountainous regions and in the northern part of the Northern Hemisphere. The numerous species of *Parmelia* (Fig. 440) are foliaceous lichens growing on trees and on rocks. *Graphis scripta* is a well-known example of the crustaceous Lichens; its greyish-white thallus occurs on the bark of trees, particularly of the Beech, on the surface of which the apothecia are disposed as narrow, black furrows resembling writing.

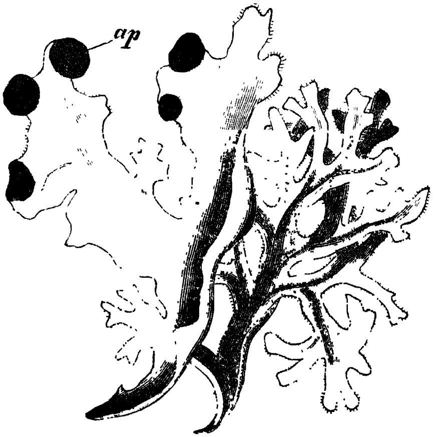


FIG. 445.—*Cetraria islandica*. *ap*, Apothecium. (Nat. size.) OFFICIAL.

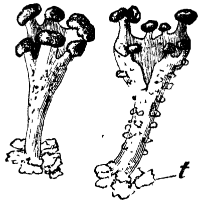


FIG. 446.—*Cladonia coccifera*. *t*, Scales of primary thallus. (Nat. size.)

A peculiar mode of development is exhibited by the genus *Cladonia*, the primary thallus of which consists of small horizontal scales attached directly to the ground; from this thallus springs an erect portion, the PODETIUM, of varying form and structure in the different species. In some cases the podetia are stalked and funnel-shaped, bearing on the margin or on outgrowths from it knob-like apothecia, which in *C. pyxidata* are brown, in *C. coccifera* (Fig. 446) bright red. In other species the erect podetia are slender and cylindrical, simple or forked; in *C. rangiferina*, Reindeer Moss, which has a world-wide distribution, particularly in the tundras of the North, the podetia are finely branched (Fig. 430), and bear the small brown apothecia at the ends of the branches. The primary thallus of this species soon disappears.

The sexual organs of the Ascolichens have been dealt with on p. 449.

2. Basidiolichenes (Hymenolichenes)

The Hymenolichenes are represented by *Cora pavonia*, of which the genera *Dictyonema* and *Laudatea* are only special growth-forms. This lichen is widely spread in the tropics, growing on the soil or on trees. The fungus of this lichen belongs to the family Thelephoreae; its flat, lobed, and often imbricated fructifications are also found entirely devoid of algae. In symbiosis with the unicellular alga *Chroococcus* it forms the fructifications of *Cora pavonia* (Fig. 447), resembling those of the Thelephoras with a channelled, basidial hymenium on the under side. Associated symbiotically, on the other hand, with filaments of the blue-green Alga *Scytonema*, if the fungus preponderates, it produces the bracket-like lichens of the *Dictyonema* form, found projecting from the branches of trees with a semicircular or nearly circular thallus, having the hymenium on the under side. When the shape of the thallus is determined by the Alga, a lichen of the *Laudatea* form occurs as felted patches of fine filaments on the bark of trees, with the hymenium on the parts of the thallus which are turned away from the light.

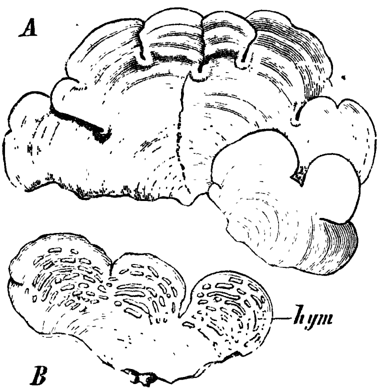


FIG. 447.—*Cora pavonia*. *A*, Viewed from above; *B*, from below; *hym*, hymenium. (Nat. size.)

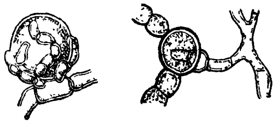


FIG. 448.—*A*, *Cladonia furcata*. Hyphae surrounding an alga (*Protococcus*). *B*, *Lempholemma dralazanum*. Branch of a hypha penetrating a cell of *Nostoc*. (After BORNET. × 600.)

OFFICIAL.—The only representative of the Lichens is *Cetraria islandica* (LICHEN ISLANDICUS). *Lobaria pulmonaria* is also used in domestic medicine.

The Manna Lichen (*Lecanora esculenta*) is a crustaceous Lichen living on rocks. The thallus falls into pieces 7-12 mm. in diameter, and is thus readily swept by the wind; it is used by the Tartars, who prepare earth-bread from it. *Cetraria islandica* (Fig. 426) also, when the bitter substances are removed by washing, may be used to make bread as well as to prepare jelly. *Cladonia rangiferina* is important as affording food for the Reindeer. Alcohol is obtained from it in Norway.

Some species particularly rich in lichen-acids are used in the preparation of the pigments orseille and litmus; there are in the first place species of *Roccella* (especially *R. Montagnei*, *R. tinctoria*, *R. fuciformis*, and *R. phycopsis*) which are collected on the coasts of the warmer oceans, and the crustaceous lichen, *Ochrolechia tartarea*, in North Europe and America.

Since the sexual reproduction is restricted to the fungus, it appears questionable whether the Lichens should be treated as a distinct class of plants. In favour of this procedure is the fact that the lichen-fungi as a rule are only able to grow under natural conditions when they have the appropriate algae at their disposal. Further, quite definite morphological characters and metabolic products appear in the symbiosis of fungus and alga; features that are exhibited by neither partner when grown in isolation.

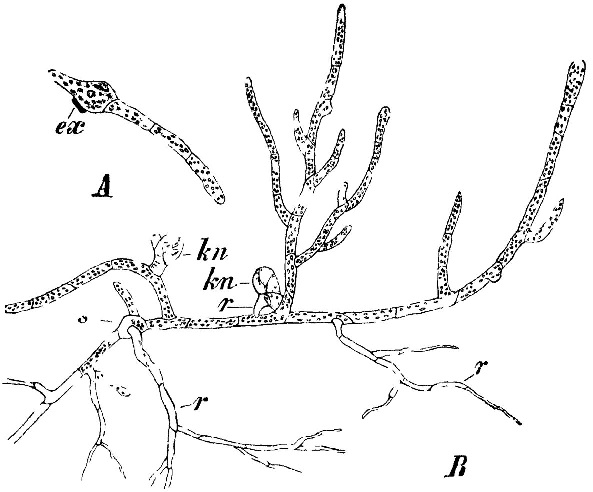


FIG. 449.—*Funaria hygrometrica*. *A*, Germinating spore; *ex*, exine. *B*, Protonema; *kn*, buds; *r*, rhizoids; *s*, spore. (Magnified. After MÜLLER-THURGAU.)

II. BRYOPHYTA (MOSSES AND LIVERWORTS) (1, 92 111)

The Bryophyta comprise two classes, the *Hepaticae* or Liverworts, and the *Musci* or Mosses. They are distinguished from the Thallophyta by the characteristic structure of their sexual organs, ANTHERIDIA and ARCHEGONIA, which are similar to those of the Pteridophyta. The Bryophyta and Pteridophyta are accordingly, in contrast to the Thallophyta, referred to collectively as *Archegoniatae*.

The course of the life-history of a Bryophyte (Fig. 481) is briefly as follows:

The unicellular, haploid spore forms on germination a filamentous green PROTONEMA (Fig. 449) which is highly developed in some groups but in others only very slightly. The plants arise as lateral buds on the protonema and have either the form of a lobed thallus (*e.g.* Figs. 460, 465, 466) or exhibit a segmentation into stem and leaves (Figs. 468, 475), they never have roots but are attached to the substratum by rhizoids. The sexual organs, antheridia, and archegonia arise on the plant of the Moss or Liverwort.

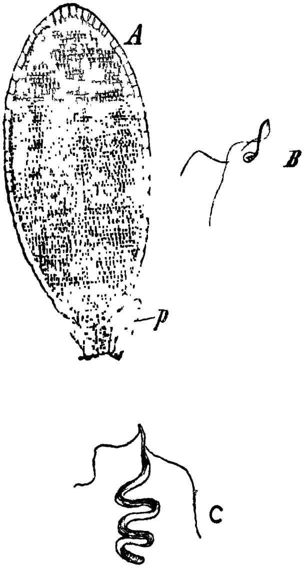


FIG 450 —*Marchantia polymorpha* *A*, Nearly ripe antheridium in section, *p*, paraphyses. *B*, Spermatozoid (*A* × 90, *B* × 600 After STRASBURGER) *C*, Spermatozoid of *Riccardia pinguis* (× 1000 After SHOWALTER)

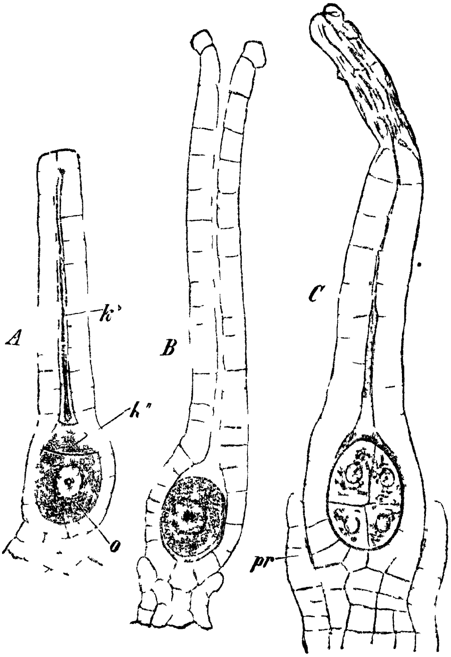


FIG 451 —*Marchantia polymorpha* *A* Young, *B*, mature archegonium, *C*, fertilised archegonium, with dividing egg cell *k*, Neck canal cells, *k'*, ventral canal cell, *o*, egg cell, *pr*, pseudo perianth (× 540 After STRASBURGER)

The ANTHERIDIA ([93] [94]) (Fig. 450) are spherical or club-shaped structures borne on multicellular stalks. The wall consists of one layer of cells, and encloses a large number of small, cubical, spermatozoid mother-cells. The antheridia open at the tip and liberate numerous spermatozoids, these have the form of short spirally-wound filaments, which mainly consist of the nucleus, and bear two long, delicate cilia close to the anterior end (Fig. 450).

The ARCHEGONIA (Fig. 451) ([93]) are short-stalked, flask-shaped organs in which a venter and neck can be distinguished. The wall of the ventral portion encloses a large central cell, which divides shortly before maturity to give rise to the egg-cell and the ventral-canal-cell. The latter is situated at the base of the neck, just below a central row of neck-canal-cells. The neck opens by the swelling of the mucilaginous contents of the uppermost cells which rupture the cuticle and often become rolled back as four lobes (Fig. 452 *B*) (95a). The canal-cells become mucilaginous. Since water is essential for the process of fertilisation, this only takes place in land-forms after wetting by rain or dew. The movement of the spermatozoids towards the archegonia, and down the neck-canal to the egg-cell is directed by particular substances diffusing from the archegonium.

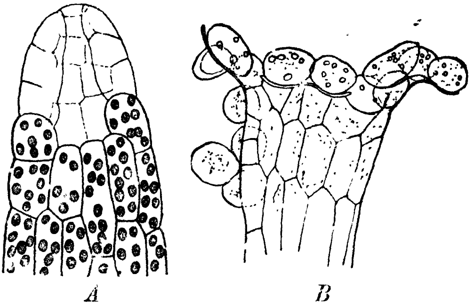


Fig. 452.—*A*, Summit of the empty antheridium of *Polytrichum* cut in half and showing the dehiscence cap. (After Goebel.) *B*, Opened neck of the archegonium of *Mnium undulatum*. (After Zielinski.)

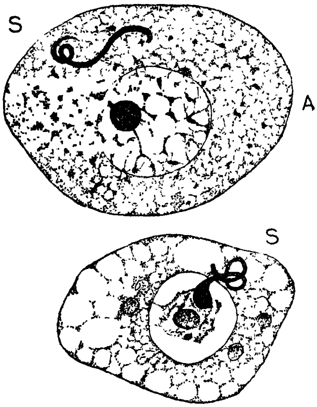


Fig. 453.—*Pellia Fabbroniana*. *A*, Spermatozoid (S) in the egg-cell *B*, entering the nucleus. (× 1050. After Showalter.)

Antheridia and archegonia are homologous organs, as is shown by the occurrence of structures of intermediate nature; the ventral-canal-cell and neck-canal-cells are to be regarded as gametes which have become functionless. The ventral-canal-cell is as a rule smaller than the egg; occasionally several egg-cells may be developed in an archegonial venter.

On fertilisation (Fig. 453) the egg-cell becomes the diploid zygote, which, without any resting period, develops directly into the embryo still enclosed in the archegonium. The basal portion of the embryo (foot) penetrates the tissue beneath the archegonium, but the main growth is towards the summit of the archegonium. This upper portion of the sporogonium forms a stalked, spherical or oval capsule (Fig. 481) in which numerous spores are produced. Since the neck-canal is too narrow to be penetrated by the growing embryo, and the wall of the venter can only keep pace with the growth of the embryo for a time, the archegonial wall ultimately becomes ruptured, as a rule, in its ventral portion (Fig. 481). When this is the case, the upper part of the archegonium is carried up by the capsule as a more or less definite cap (CALYPTRA), while its lower part remains as a sheath around the stalk of the sporogonium (Figs. 471 *C*, 472, 473).

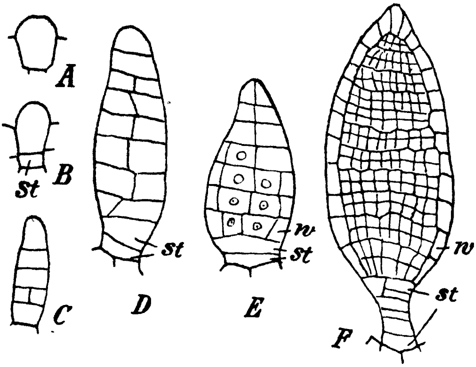


FIG. 454.—Development of the antheridium in *Fegatella conica*, one of the Marchantiaceae. *A*, Unicellular stage. *B*, The stalk-cell (*st*) cut off. *C*, *D*, Antheridium divided into a row of cells which in turn are divided by longitudinal walls. *E*, Cutting off of the layer of cells to form the wall (*w*). *F*, Advanced stage of development. (*A*–*E* × 400; *F* × 220. After BOLLETER.)

The spores arise in groups of four (TETRADS) from the inner tissue of the capsule which is termed the ARCHESPORIUM. This results by two successive cell-divisions of the spore-mother-cells which have separated from one another and rounded off; in these divisions reduction in number of the chromosomes and sex-determination is effected. The wall of the spore has two layers, consisting of a delicate inner endospore and a cutinised exospore; the latter is ruptured on germination. The spores give rise, according to the species, to monoecious or dioecious plants.

The Bryophyta are characterised by a great power of regeneration from cut portions of all the organs. Vegetative reproduction by means of gemmae, etc., is widespread; they arise on the thallus, on stems, on leaves, and on the protonema in a great variety of ways, becoming separated later (97b).

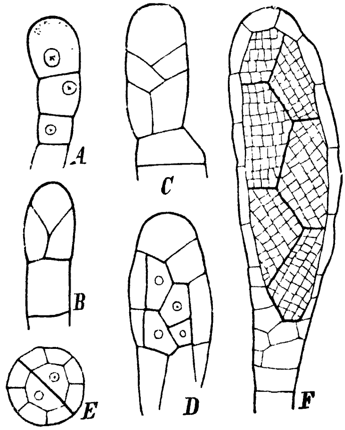


FIG. 455.—Development of the antheridium of a Moss. *Funaria hygrometrica*. *A*, Primordium of an antheridium divided into four cells. *B*, Formation of the apical cell from the uppermost cell. *C*, Division of the apical cell. *D*, The separation of the wall-layer and the cells that will give rise to the spermatogenous tissue. *E*, Same stage in transverse section. *F*, Older stage. (After D. CAMPBELL.)

The Bryophyta include two well-marked classes; the Liverworts (Hepaticae) and the Mosses (Musci). These are distinguished, in addition to characters of the vegetative plant-body, by the mode of development of the sexual organs and of the sporogonium.

The antheridia and archegonia always develop from superficial cells.

In the Liverworts the main features of the development of the antheridium are as follows: A superficial cell divides transversely into disc-shaped segments, and each of the latter is divided by walls standing at right angles to one another into four cells. In these quadrants tangential walls separate the peripheral cells forming the antheridial wall from inner cells which go to form the spermatogenous tissue (Fig. 454 *A*-*F*).

In the Mosses on the other hand, after preliminary transverse divisions a two-sided initial cell is defined by two oblique walls in the uppermost segment; this cuts off two rows of segment-cells in which the separation cells of the wall-cells from inner cells, giving rise to spermatogenous tissue, follows (Fig. 455 *A*-*F*).

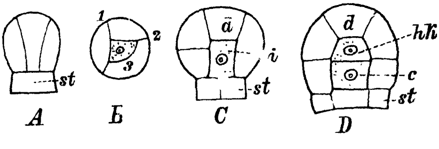


Fig. 456.—Development of the archegonium of a Liverwort. *A* (longitudinal section) and *B* (transverse section), showing the upper cell divided by three walls. *C*, The central cell divided into cap-cell (*d*) and internal cell (*i*). *D*, The internal cell divided into the cells which will give rise to the neck-canal-cells (*hk*), and the ovum and ventral-canal-cells (*c*) respectively; *st*, young stalk. (After Goebel.)

The opening of the antheridia takes place at their tips; in Liverworts by all the cells of the wall becoming mucilaginous and swelling, in the Mosses by means of a special cap of cells, the mucilaginous contents of which swell and rupture the cuticle (Fig. 452 *A*).

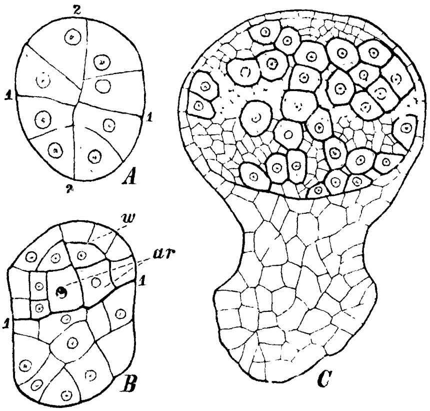


Fig. 457.—Development of the sporogonium of *Corsinia marchantioides*, one of the Marchantiaceae. *A*, The zygote divided into 16 cells. *B*, The lower half of the embryo developing as foot, the upper as capsule; *w*, wall-cells; *ar*, archesporium. (× 170.) *C*, Older sporogonium. The archesporium has given rise to spore-mother-cells and small sterile cells which in *Corsinia* do not develop further into elaters. (× 90.) (After K. Meyer.)

The spermatozoids (Fig. 450, *B*, *C*) react chemotactically, in the case of the Liverworts, to proteid substances, etc., and in the Mosses to solutions of cane sugar (^{956}).

Development of the Archegonia. In Liverworts a superficial cell divides into a lower cell, which forms the stalk, and an upper cell. In the latter three longitudinal walls separate three outer cells from a median cell; the latter is then divided by a transverse wall into a cap-cell and an inner cell. The outer cells give rise to the wall of the neck and venter of the archegonium; from the inner cell are derived the neck-canal-cells (4 or 8), the ventral-canal-cell and the egg-cell (Fig. 456).

In the Mosses, on the other hand, a two-sided initial cell is established, the segments of which go to form the stalk. The terminal two-sided cell then divides by three oblique walls and one transverse wall to give rise to three peripheral wall-cells, a three-sided terminal cell with a transverse lower wall, and below the latter a centrally placed cell. This central cell gives rise to the egg, the ventral-canal-cell and some of the neck-canal-cells. By the segmentation of the terminal cell the wall-cells of the neck and the uppermost neck-canal-cells (10-30 or more) are produced.

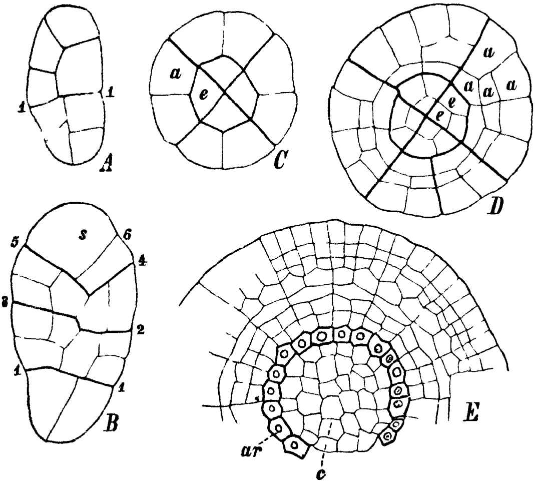


FIG. 458.—Development of the sporogonium of the Moss, *Funaria hygrometrica*. *A*, *B*, Longitudinal sections showing first stages in the development from the zygote *s*, apical cell. *C-E*, Transverse sections: *C*, division into endothecium (*e*) and amphithecium (*a*); *D*, further divided stage; *E*, older sporogonium, in the endothecium of which the outermost layer is distinct as the archesporium (*ar*) from the columella (*c*). (After CAMPBELL.)

In the DEVELOPMENT OF THE SPOROGONIUM (96) in the Liverworts the zygote divides transversely and longitudinally into eight cells, then by radial walls into sixteen cells, and these then divide by periclinal walls into outer and inner cells (Fig. 457). From the lower half of this embryo the foot and the short seta originate and from the upper portion the capsule. The central cells of the latter (ARCHESPORIUM) give rise to the sporogenous tissue. Each cell of the archesporium becomes divided into a narrower and a broader daughter-cell. The broader cells, either directly or after further divisions, become spore-mother-cells. The narrow cells, as a rule, grow into fibre-like structures, with spiral thickening bands, the elaters, which, on the opening of the capsule, loosen and disperse the spores by their hygroscopic movements.

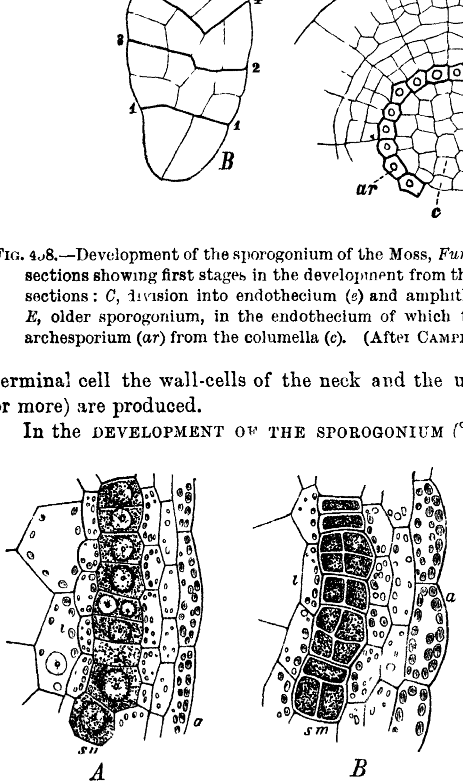


FIG. 459. — *Funaria hygrometrica*. Transverse section through the archesporium (*A*, *su*), and the groups of still connected spore-mother-cells derived from it (*B*, *sm*). (After GOEBEL.)

In the Mosses the zygote also divides transversely to begin with, forming an elongated embryo composed of transversely placed segments. In typical cases, oblique walls then form in the uppermost cell and determine a two-sided apical cell (Fig. 458 *A*, *B*), which proceeds to cut off segments to the right and left, and these divide further. In the segments which go to form the capsule there is first a longitudinal division; in the resulting quadrants periclinal walls then separate outer cells (amphithecium) from inner cells (endothecium) (Fig. 458 *C*, *D*). The outermost layer of cells of the endothecium becomes the archesporium (*E*), which at once divides to give rise to spore-mother-cells; these later divide to give rise to four spores from each. There are no sterile cells or elaters (Fig. 459). The inner cells of the endothecium on the other hand, are not concerned with the production of spores, but form a strand of sterile tissue (the COLUMELLA), (Figs. 458 *E*, 461 *E*), which serves for conduction. This is surrounded by the spore-sac.

Deviations from the types described occur in the various orders and will be referred to, so far as is necessary, in the following account of the groups.

CLASS I

Hepaticae (Liverworts) (1, 92, 93, 96-103)

Most Liverworts inhabit moist situations and have a corresponding hygromorphic structure. True aquatic forms are, however, only sparingly represented. Some delicate forms grow among Mosses. Forms which live in extremely dry habitats on the bark of trees, on rocks, or on the ground are relatively infrequent; these have xeromorphic structure and arrangements for the storage of water. Among the epiphytes, those that grow on leaves in tropical forests (epiphyllous liverworts) are noteworthy. As a rule, the Liverworts play an inconsiderable part in the composition of cryptogamic plant-formations.

In the Liverworts, the protonema is always developed merely as a short tube.

The Hepaticae are divided, according to the structure of the sporogonium and the segmentation exhibited by the sexual plant, into three orders, the Anthocerotales, Marchantiales, and the Jungermanniales.

Order 1. Anthocerotales (101)

This isolated group, including only a few forms, may be regarded as a primitive order of Bryophyta. The sporogonium is characterised by a more complicated internal construction than in the other Liverworts, in which it has undergone progressive simplification.

The GAMETOPHYTE has the form of a lobed thallus, which is firmly anchored to the soil by means of rhizoids. The cells of the thallus contain, in contrast to those of other Bryophyta, a single large chloroplast with a pyrenoid resembling the chloroplasts of some Algae. On the lower surface, and less commonly on the upper, typical stomata with two guard-cells occur. The ANTHERIDIA arise singly or in groups of four, by the division of a cell lying below the epidermis (Fig. 461); they remain enclosed in cavities beneath the upper surface of the thallus until maturity. The origin of the antheridia thus differs from what is the case in all other Archegoniatae in being endogenous; a superficial cell divides into an outer segment, forming the roof of the cavity (*d*), and an inner one (*a*), which becomes the mother-cell of the antheridia. The cavity opens at maturity by mucilage-formation in the cells of the outer wall. The ARCHEGONIA are sunk in the upper surface of the thallus; after fertilisation they become covered over by a many-layered wall (MARSUPIUM) formed by the growth of the adjoining tissue. This envelope is afterwards ruptured by the elongating capsule, and forms a sheath at its base. The SPOROGONIUM consists of a swollen foot and a long, pod-shaped capsule ; it has no stalk. The superficial cells of the foot grow out into rhizoid-like papillae. The capsule splits longitudinally into two valves, and has a central hair-like columella formed of a few rows of sterile cells (Fig. 461). The columella does not extend to the apex of the capsule, but is surmounted by a narrow layer of sporogenous cells. Elaters also occur ; they are multicellular, variously shaped, and often forked. The sporogonia, unlike those of all other Hepaticae, do not ripen simultaneously throughout their whole length, but from the tips downwards, and continue to elongate by basal growth. The wall of the sporogonium possesses stomata, which do not occur in other Liverworts; chlorophyll is present in its cells.

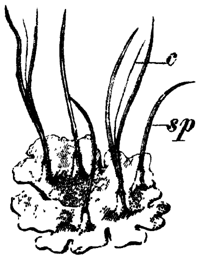


FIG. 460.—*Anthoceros laevis*. *sp*, Sporogonium ; *c*, columella. (Nat. size.)

On the under side of the thallus, cavities filled with mucilage occur beneath the stomata. *Nostoc* filaments penetrate into these cavities, and develop into endophytic colonies (111a).

Order 2. Marchantiales (102)

The Liverworts included in this order in many genera have a decidedly complicated structure. *Marchantia polymorpha*, found growing on damp soil, may

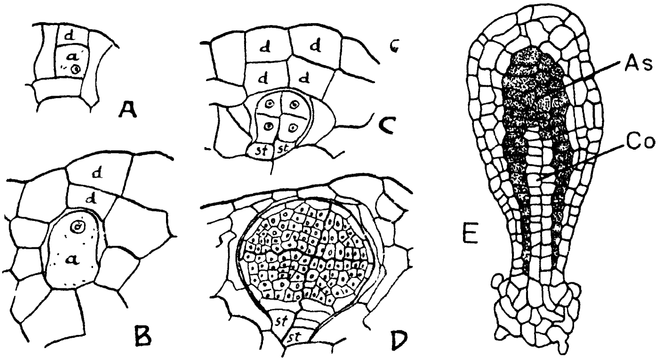


FIG. 461.—*Anthoceros Pearsoni*. Development of the endogenous antheridium. *d*, Covering cells ; *st*, stalk-cells ; *a*, young antheridium. *E*, *Notothylas*. Young sporogonium. *Co*, columella : *As*, archesporium. (After D. CAMPBELL.)

serve as an example. It forms a flat, deeply-lobed, dichotomously-branched thallus, about two centimetres wide, and having an inconspicuous midrib (Fig. 464 *A*, Fig. 465 *A*). From the under side of the thallus spring unicellular RHIZOIDS, some of which have smooth walls and serve mainly to attach the thallus, while others have conical thickenings projecting into the cell-cavity (Fig. 30) ; these peg-rhizoids are collected to form a wick-like strand below the midrib. The thallus is provided also with VENTRAL SCALES, consisting of a single layer of cells. The dorsiventrality of the thallus is further shown by its complicated anatomical structure. With the naked eye it may be seen that the upper surface of the thallus is divided into small rhombic areas. Each area is perforated by a central air-pore leading into a corresponding AIR-CHAMBER immediately below (Fig. 462 *A*, *B*). The lateral walls of the air-chambers determine the configuration of the rhombic areas. The air-pore in the roofing wall of each chamber is in the form of a short canal, bounded by a wall formed of several tiers of cells, each tier comprising four cells. Numerous short filaments, consisting of rows of nearly spherical cells containing chlorophyll grains, project from the floor of the air-chambers and perform the functions of assimilating tissue. Chlorophyll grains are found also in the walls and roof of the chambers, but only in small numbers. The intensity of the illumination exercises a great influence on the formation of air-chambers; when the illumination is very weak they may not occur at all. The epidermis on the under side of the thallus is formed of one layer of cells. The tissue below the air-chamber layer is devoid of chlorophyll, and consists of large parenchymatous cells, which serve as storage cells.

Small cup-shaped outgrowths, with toothed margins, the gemmiferous receptacles or GEMMA-CUPS, are generally found situated on the upper surface of the thallus

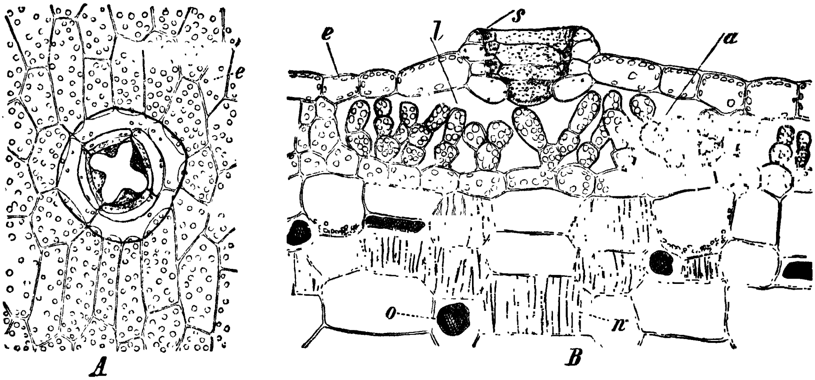


FIG. 462.—Surface view and transverse section of the thallus of *Marchantia polymorpha*. *A*, shows an air-pore from above, and *B*, the pore in section ; *e*, epidermis ; *s*, cells bounding the air-pore ; *l*, air-chamber ; *a*, assimilation tissue ; *o*, oil-bodies ; *w*, water-storage tissue. (After STRASBURGER and KOERNICKE. × 240.)

over the midribs (Fig. 464 *b*). These contain a number of stalked GEMMAE, flat bodies of a green colour. The gemmae arise by the protrusion and repeated division of a single epidermal cell (Fig. 463); at maturity they become detached from the stalk (at *x*, Fig. 463 *D*). They are provided with two growing points, one at each of the marginal constrictions, from which their further development into new plants proceeds. On cross-section (*E*) they are seen to be composed of several layers of cells; some of the cells are filled with oil bodies (*D*, *o*), while from other colourless cells rhizoids develop. Cells containing oil are also present in the mature thallus, and are of frequent occurrence in all the Hepaticae. By means of the abundantly-developed gemmae *Marchantia* is enabled to multiply vegetatively to an enormous extent. The dorsiventrality of the plants developed from the gemmae is determined by the influence of light.

The SEXUAL ORGANS, antheridia and archegonia, are borne on special erect branches of the thallus. The reproductive branches, which are contracted below into a stalk, expand above into a stellately branched upper portion. In this species, which is dioecious, the antheridia and archegonia develop on different plants.

The branches producing the male organs terminate in lobed discs, which bear the antheridia on their upper sides in flask-shaped depressions, each containing an ANTHERIDIUM (Fig. 464 *B*). The depressions, into each of which a narrow canal leads, are separated from each other by tissue provided with air-chambers. The spermatozoids collect in a drop of water on the disc, the margin of which serves to retain the water.

The female branches terminate each in a nine-rayed disc (Fig. 465 *A*). The upper surface of the disc, between the rays, becomes displaced downwards in the process of growth, and, as the archegonia are borne on these portions, they seem to arise from the under-side of the disc. The ARCHEGONIA are disposed in radial rows between the rays, each row being surrounded by a toothed lamella or sheath (perichaetium) (*B*, *C*, *h*). For structure of the archegonia see Fig. 451 and description.

FERTILISATION takes place during rain, the raindrops splashing the liquid on the male discs which contains the spermatozoids on to the female receptacles. The epidermal cells of the latter project as papillae and constitute a superficial capillary system in which the spermatozoids are conducted to the archegonia.

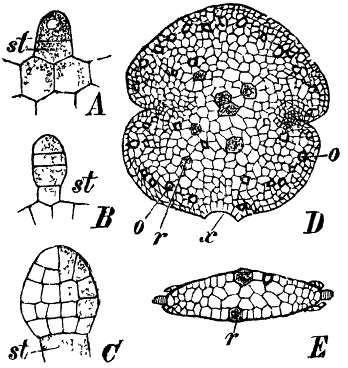


FIG. 463.—*Marchantia polymorpha*. *A*-*C*, Successive stages in the formation of a gemma; *st*, stalk-cell; *D*, surface view; *E*, transverse section of a gemma; *x*, point of attachment to stalk; *o*, oil-cells; *r*, colourless cells with granular contents, from which the rhizoids will develop. (*A*-*C* × 275; *D*-*E* × 65. After KNY.)

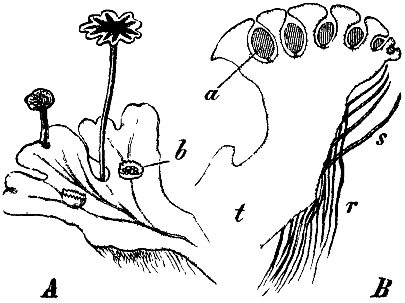


FIG. 464.—*Marchantia polymorpha*. *A*, A male plant, with antheridiophores and gemma-cups *b* (nat. size). *B*, Section of young antheridiophore; *a*, antheridia; *t*, thallus; *s*, ventral scales; *r*, rhizoids. (Somewhat magnified.)

The fertilised egg-cell gives rise to a multicellular embryo (Fig. 451 *C*), and this, by further division and progressive differentiation, develops into a stalked, oval SPOROGONIUM. The capsule of the sporogonium is provided with a wall consisting of one layer of cells except at the apex, where it is two-layered; the cell-walls have thickened bands. The capsule ruptures at the apex, the lid falling off and the wall splitting into a number of recurved teeth. The ripe capsule, before the elongation of the stalk, remains enclosed in the archegonium wall (Fig. 465 *D*, *aw*), which, for a time, keeps pace in its growth with that of the capsule. As the stalk elongates, the archegonial wall or calyptra is broken through and remains behind, as a sheath, at the base of the sporogonium (*E*, *c*). The capsule is surrounded also by the pseudo-perianth, an open sac-like envelope which grows, before fertilisation, out of the short stalk of the archegonium (Fig. 451 *C*, *pr*; Fig. 465 *D*, *E*, *p*). The capsule contains spores (some 300,000) and elaters (Fig. 465 *F*, *G*).

Marchantia was formerly used in the treatment of diseases of the liver; this fact explains the origin of the name Liverwort.

The **Ricciaceae** (103) exhibit a simplification of the sporogonium and connect

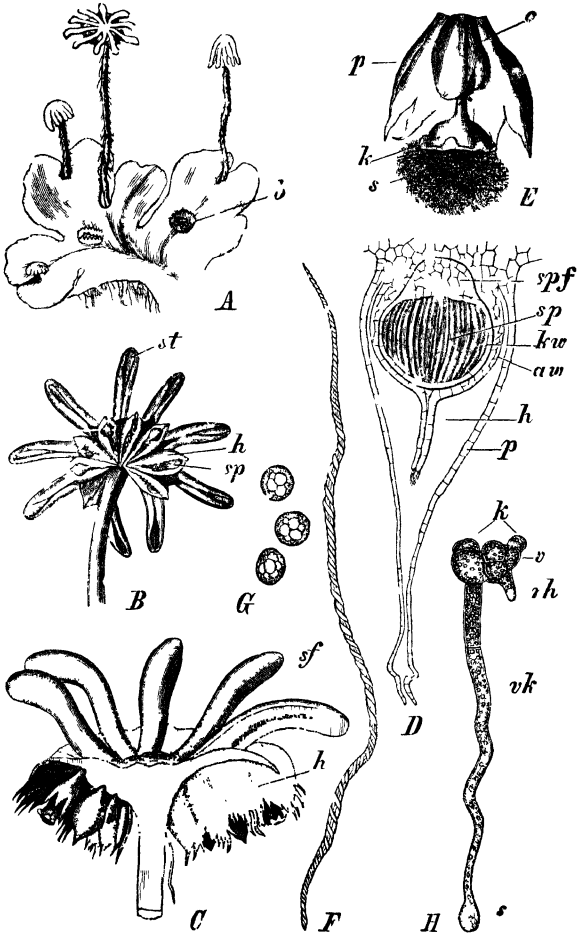


FIG 465 —*Marchantia polymorpha* *A*, A female plant, with four archegoniophores of different ages, *b* gemma cups (nat size) *B*, Under side of receptacle *st* rays *h* sheath, *sp* sporogonium (×3) *C*, Half of a receptacle, divided longitudinally (×5) *D*, Longitudinal section of a young sporogonium, *spf*, the foot, *sp*, sporogenous tissue, *kw*, wall of capsule, *aw*, wall, and *h*, neck, of archegonium, *p*, pseudo perianth (×70) *E*, Ruptured sporogonium *k*, capsule, *s*, spores and elaters, *p*, pseudo perianth, *c*, archegonial wall (×10) *F*, An elater *G*, Ripe spores (×315) *H*, Germinating spore (*s*), *vk*, germ-tube *k*, germ disc, with the apical cell *v* and rhizoid *rh* (×100) (*C*, *E* after BISCHOFF, *B*, *D*, *F* *H* after KNY)

on as reduced forms to the more simply constructed Marchantiaceae. The dichotomously-lobed or cleft thallus forms small rosettes, and grows on damp soil, or floating, or submerged in water. Differences in habit are found in relation to the situation in which the plants occur (Fig. 466 *B, C*). The antheridia and archegonia are sunk in the surface of the upper side of the thallus. From the fertilised egg-cell is developed a spherical sporogonium which has no stalk. The wall of the sporogonium consists of a single layer of cells; it becomes disorganised during the ripening of the spores, which are eventually set free by the rupture and disintegration of the venter and the surrounding cells of the thallus. There are no elaters, all the cells of the archesporium becoming spore-mother-cells.

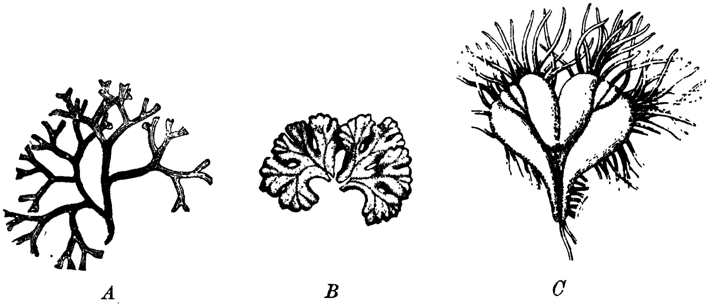


FIG. 466.—*A*, *Riccia fluitans*; submerged floating form. *B*, *Riccia natans*; land-form. (Nat. size. *B* after GOEBEL.) *C*, *Riccia natans*; floating form with long ventral scales. (After BISCHOFF. ×2.)

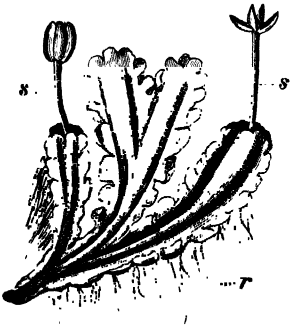


FIG. 467.—*Blasia pusilla*. *s*, Sporogonium; *r*, rhizoids. (× 2.)

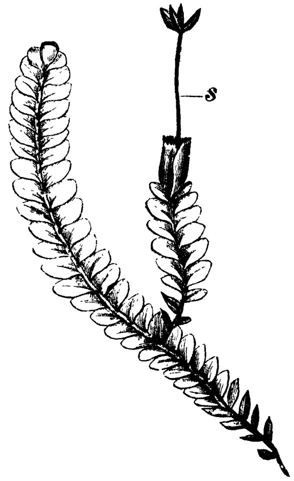


FIG. 468.—*Plagiochila asplenioides*. *s*, Sporogonium. (Nat. size.)

Order 3. Jungermanniales

These are usually small forms which grow on the ground or on tree-trunks, and in the tropics on the surface of living leaves. In the simplest forms of this order the thallus is broadly lobed, similar to that of *Marchantia* (*e.g. Pellia epiphylla*, frequently found on damp ground); or, like that of *Riccia fluitans*, it is narrow and ribbon-shaped, and at the same time profusely branched (*e.g. Metzgeria furcata*, Fig. 91). In other forms, again, the broad, deeply-lobed thallus has an evident midrib, and its margins, as in the case of *Blasia pusilla* (Fig.

467), exhibit an incipient segmentation into leaf-like members. The majority of Jungermanniaceae, however, show a distinct segmentation into a prostrate or ascending, dorsiventral stem and leaves (Fig. 468). The latter consist of one layer of cells without a midrib, and are inserted with obliquely directed laminae in two rows on the flanks of the stem. Many genera (*e.g. Frullania Tamarisci*, a delicately-branched Liverwort of a brownish colour occurring on rocks and tree-trunks) have also a ventral row of small scale-like leaves or amphigastria (Fig. 469). The dorsal leaves are frequently divided into an upper and lower lobe. In species growing in dry places, like *Frullania Tamarisci*, the lower lobe may be modified into a sac, and serves as a capillary water-reservoir. The leaves regularly overlap each other; they are then said to be OVERSHOT, when the posterior edges of the leaves are overlapped by the anterior edges of those next below (*Frullania*, Fig. 469), or UNDERSHOT, if the posterior edges of the leaves overlap the anterior edges of the leaves next below (*Plagiochila*, Fig. 468).

The development of the ANTHERIDIUM differs somewhat from the type described in the introduction above. Only the uppermost of the transverse segments into which the young antheridium is divided forms the body of the antheridium. This cell is first divided into two by a vertical wall. In each of these, two oblique longitudinal walls form and thus the wall of the antheridium is separated from the spermatogenous tissue.

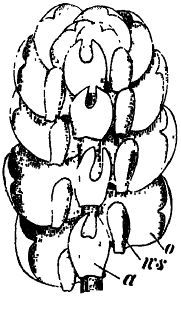


FIG. 469.—Part of a shoot of *Frullania Tamarisci*, seen from below. *o*, Dorsal leaves with the lower lobes (*ws*) modified as water-sacs; *a*, amphigastrium. (× 35.)

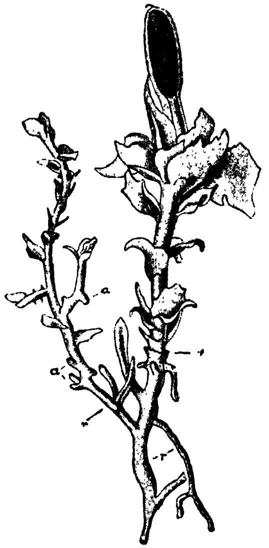


FIG. 470.—*Haplomitrium Hookeri*. *a*, Origin of a new shoot; *r*, rhizome; *o*, lower limit of the aerial shoot. (After GOTTSCHE.)

The fertilised egg first divides transversely to give rise to a row of cells; the lowest of these forms a suctorial organ which is sometimes multicellular, but as a rule unicellular. The upper cells give rise to the foot and the stalked capsule.

The SPOROGONIUM is already fully developed before it is pushed through the apex of the archegonial wall by the elongating delicate stalk. It has a spherical capsule which on rupturing splits into four valves. No columella is formed in the capsule; but it always produces elaters in addition to spores. In some genera (*Pellia*, *Aneura*) there are special elaterophores which consist of groups of sterile cells resembling the elaters. The wall of the capsule (usually two or several cells thick) consists of cells with annular or band-like thickenings, or the walls are uniformly thickened with the exception of the outermost walls. Dehiscence is dependent on the cohesive power of the water in these cells pulling the outer walls into the cavity.

According to the position of the sexual organs and sporogonium the Jungermanniales are divided into groups. 1. In the **Anakrogynae** the apex is not used up in the formation of the archegonia, and the sporogonia are situated on the dorsal surface and are surrounded by a sheath-like outgrowth of the thallus forming a perichaetium. To this group belong the thalloid forms (*Pellia, Metzgeria*) and others showing a transition to the foliose forms (*Blasia*). 2. In the **Akrogynae**, on the other hand, the archegonia and the sporogonium stand at the end of the main stem, or of a branch, and are surrounded by a perianth formed of modified leaves. To this group belong the dorsiventral leafy forms, *e.g. Plagiochila, Frullania*, and *Jungermannia*, a genus with numerous species. 3. The **Haplomitrieae** hold an isolated position, but appear to exhibit the closest connection with the Anakrogynae. This order contains only two genera, *Calobryum*, occurring in the tropics, and *Haplomitrium*. The single species of the latter genus, *H. Hookeri* (Fig. 470), occurs in Europe, and possibly is a survival of pre-glacial Liverworts. The Calobryaceae differ from all other Liverworts in the radial construction of their shoot, which bears three rows of leaves. The sexual organs form terminal groups in *Calobryum*; in *Haplomitrium* they occur between the upper leaves.

CLASS II

Musci (Mosses) (1, 92, 93, 104-111)

The Mosses include a large number of forms distributed in all parts of the world. They grow on dry soil, in swamps, on rocks, on tree-trunks and in tropical forests, also as epiphytes on the branches, and less commonly in water; their structure is correspondingly various. Close tufts or masses are especially characteristic of dry habitats, while the typical inhabitants of the soil of woods have a looser mode of growth. In the moist mountain forests of the tropics and sub-tropics Mosses often grow in considerable masses surrounding the branches or hanging in long veil-like masses from them (105). The Bog-Mosses form extensive growths on moors, as also do others (especially *Polytrichum*) on the moist soil in the arctic moss-tundras.

The profusely-branched protonema of the Mosses appears to the naked eye as a felted growth of fine, green filaments (Fig. 449). Branched filaments without chlorophyll extend into the soil, and in these rhizoids the oblique position of the cell-walls is characteristic. The young moss-plants are developed on the protonema as small buds, which arise as protrusions of cells of the filament, usually from the basal cell of one of the branches. The protrusion is cut off by a transverse septum, and, after the separation of one or two stalk-cells, the three-sided pyramidal apical cell of the moss-plant is delimited in the enlarged terminal cell (106a). The moss-plants are always differentiated into stem and leaf. The Mosses may be readily distinguished from the foliose Jungermanniaceae by the spiral arrangement of their small leaves, which are rarely arranged in two rows.

In Mosses which have prostrate stems, the leaves, although arranged spirally, frequently assume a somewhat outspread position, and all face one way, so that in such cases a distinction between an upper and a lower side is manifested, but in a manner different from that of the Liverworts.

The SEXUAL ORGANS are always borne in groups at the apices either of the main axes or of small, lateral branches, surrounded by the upper leaves of the latter, which frequently have a distinctive structure, and are known as the PERICHAETIUM (Fig. 475). Between the sexual organs there are usually present a number of multicellular hairs or paraphyses, the terminal cells of which are often enlarged and spherical. The moss-plants may be monoecious, in which case both kinds of sexual organs are borne on the same plant either in the same or different receptacles; or dioecious, and then the antheridia and archegonia arise on different plants. In some dioecious Mosses the male plants are very small dwarf-plants, which, after forming a few small leaves, proceed to produce antheridia (^{107}).

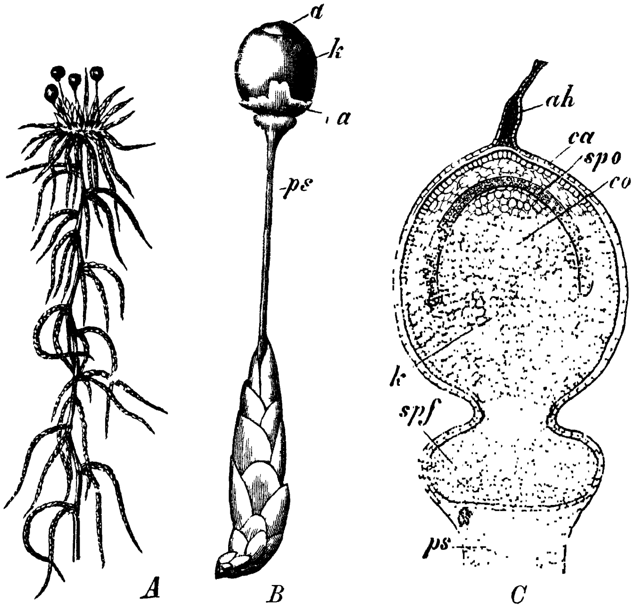


FIG. 471.—*Sphagnum fimbriatum*: *A*, A shoot with four ripe sporogonia. *Sphagnum squarrosum* *B*, A lateral shoot with a terminal sporogonium; *ca*, ruptured calyptra; *d*, operculum. *Sphagnum acutifolium*: *C*, a young sporogonium in longitudinal section, *ps*, pseudopodium *ca*, archegonial wall or calyptra, *ah*, neck of archegonium, *spf*, foot of sporogonium; *k*, capsule; *co*, columella; *spo*, spore-sac with spores. (*B* and *C* after W. P. SCHIMPER; *A*, nat. size; the other figures magnified.)

The archegonia and antheridia of Mosses differ in their development from those of other Archegoniatae by being formed by the segmentation of an apical cell, which in the case of the antheridia is two-sided, and in that of the archegonia, three-sided.

After fertilisation the lower portion of the embryo which serves as an absorbent organ or foot penetrates the proliferating tissue of the stalk of the archegonium or even into the tissue of the upper portion of the stem.

The SPOROGONIUM of the Mosses (^{108}) develops a capsule with an axial COLUMELLA consisting of sterile tissue (Fig. 477). The spore-sac surrounds the columella, which conducts and accumulates food-material and water for the developing spores. Elaters are never formed. In the young sporogonium outside the spore-sac a well-developed assimilating tissue is present; this is bounded by water-storage tissue and an epidermis. In most Mosses stomata are found on the lower part of the capsule. The ripe capsule exhibits a variety of peculiar structures to facilitate the opening and the distribution of the

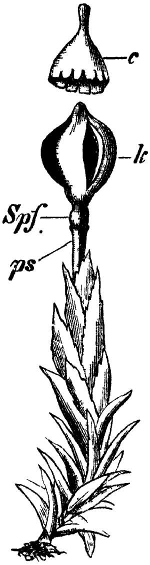


FIG. 472.—*Andreaea petrophila*. *ps*, Pseudopodium; *Spf*, foot; *k*, capsule; *c*, calyptra. (× 12.)

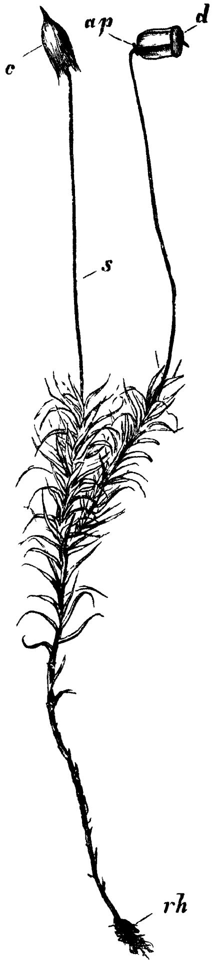


FIG. 473.—*Polytrichum commune*. *rh*, Rhizoids; *s*, seta; *c*, calyptra; *ap*, apophysis; *d*, operculum. (Nat. size.)

spores. The stalk or SETA raises the capsules so that the spores are readily dispersed by wind. The remains of the archegonial wall are carried up on the capsule as the well-developed CALYPTRA. Distinctive variations in the mode of development and structure of the capsules are exhibited by the three orders of the Musci: *Sphagnales*, *Andreaeales*, and *Bryales*.

Order 1. Sphagnales (109)

The Sphagnaceae, or Bog Mosses, are the only family and include only a single genus, *Sphagnum*, containing many species. The Bog Mosses grow in swampy places, and form large tussocks saturated with water. The upper extremities of the stems continue their growth from year to year, while the lower portions die away and become eventually converted into peat. The protonema which is developed from the spore is not filamentous, but forms a small, lobed, flat, thalloid structure.

The stems are profusely branched. Of the numerous lateral branches arising from each of the shoots, some grow upwards and form the apical tufts or heads at the summits of the stems; others, which are more elongated and flagelliform in shape, turn downwards and envelop the lower portions of the stem (Fig. 471 *A*). Every year one branch below the apex develops as strongly as the mother-shoot, so that the stem becomes falsely bifurcated. By the gradual death of the stem from below upwards the daughter-shoots become separated from it, and form independent plants. The cortex of the stem consists of three or four layers of empty cells with perforations in their walls which have annular or spiral thickenings; these cells absorb water readily. Similar cells are present in the leaves, where they occupy the meshes of a network of elongated living cells with chloroplasts; the two kinds of cells make up the one-layered leaf. This peculiar capillary apparatus is of use in the absorption of water.

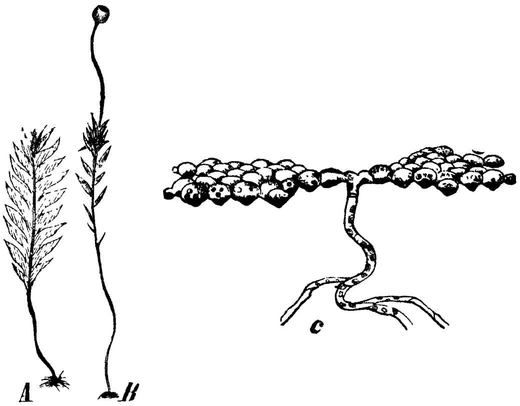


FIG. 474.—*Schistostega osmundacea.* *A*, Sterile; *B*, fertile plant. (× 5.) *C*, Protonema. (× 90. After NOLL.)

Special branches of the tufted heads are distinguishable by their different structure and colour; on these the sexual organs are produced. The male branches give rise, beside the leaves, to spherical stalked antheridia. The archegonia are borne at the tips of the female branches. In contrast to other Mosses, and in agreement with Liverworts, they do not grow by means of an apical cell cutting off three rows of segments. The sporogonium develops a short stalk with an expanded foot (*B*, *C*), but remain for a time enclosed by the archegonial wall or calyptra. The archesporium does not arise from the endothecium but from the innermost layer of the amphithecium. Upon the rupture of the archegonium, the calyptra persists as in the Hepaticae, at the base of the sporogonium. The capsule is spherical and has a dome-shaped columella, which in turn is overarched by a hemispherical spore-sac (*spo*); this is possibly an indication of affinity with the Anthocerotales. It opens by the removal of an operculum. The ripe sporogonium is borne upon a prolongation of the stem-axis, the pseudopodium, which is expanded at the top to receive the foot. The pseudopodium develops after the fertilisation of the archegonium.

Order 2. Andreaeales

The Andreaeales comprise only the one genus, *Andreaea*, small, brownish, caespitose Mosses growing on rocks. The sporogonium is also terminal in this order. The capsule, at first provided with a calyptra, splits into four longitudinal valves (schizocarpous), which remain united at the base and apex (Fig. 472). The stalk is short, and is expanded at the base into a foot (*Spf*), which in turn is borne, as in *Sphagnum*, on a pseudopodium (*ps*). The protonema is to begin with, a small group of cells, and as it develops becomes ribbon-shaped.

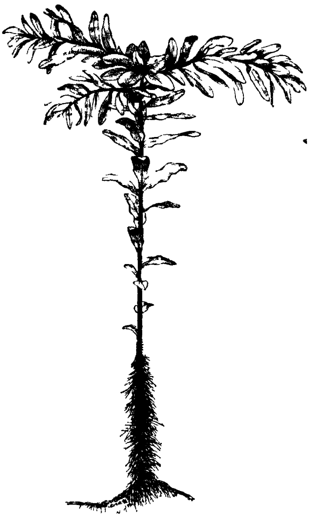


Fig. 475.—*Mnium undulatum* Orthotropous shoot terminating in a male receptacle surrounded by involucral leaves The lateral shoots are plagiotropous (After Goebel)

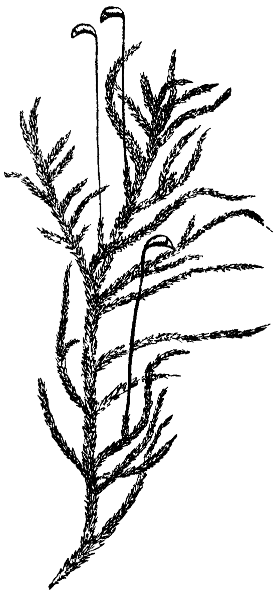


Fig 476.—*Scleropodium purum* (Nat size)

Order 3. Bryales ([110])

In this order, which includes the great majority of all the true Mosses, the moss-capsule attains its most complicated structure. The ripe SPOROGONIUM, developed from the fertilised egg, consists of a long stalk, the SETA (Fig 473 *s*), with a FOOT at its base, sunk in the tissue of the mother-plant, and of a CAPSULE, which in its young stages is surmounted by a hood or CALYPTRA. The calyptra is thrown off before the spores are ripe. It consists of one or two layers of elongated cells, and originally formed part of the wall of the archegonium; this, at first, enclosed the embryo, growing in size as it grew, until, finally ruptured by the elongation of the seta, it was carried up as a cap, covering the capsule. It consists of several layers of cells and, especially in forms which occupy dry habitats, bears hairs that correspond to protonemal threads of limited growth. In some Mosses (*e.g. Funaria*) the young calyptra is distended and serves as a reservoir of water for the young sporogonium ([110a]). The upper part of the seta, where it joins the capsule, is termed the APOPHYSIS. In *Mnium* (Fig. 479 *A*, *ap*) it is scarcely distinguishable, but in *Polytrichum commune* it has the form of a swollen ring-like protuberance (Fig. 473 *ap*), while in species of *Splachnum* it dilates into a large collar-like structure of a yellow or red colour. In the latter genus, flies, attracted by the bright colour of the apophysis and by the odour, serve to distribute the spores ([110b]). The capsule is traversed throughout its length by the columella, around which is the spore sac. Between the spore-sac and wall of the capsule comes an air-space. The upper part of the capsule becomes converted into a lid or operculum which is sometimes drawn out into a projecting tip. At the margin of the operculum a narrow zone of epidermal cells termed the ring or ANNULUS becomes specially differentiated. The cells of the annulus contain mucilage, and by their expansion at maturity assist in throwing off the lid. In most Mosses the mouth of the dehisced capsule bears a fringe, the PERISTOME, consisting usually of tooth-like appendages, but in others this is wanting.

The peristome of *Mnium hornum* (Fig. 479), which will serve as an example, is double; the outer peristome is formed of 16 pointed, transversely striped teeth inserted on the inner margin of the wall of the capsule. The inner peristome lies just within the outer, and consists of cilia-like appendages, which are ribbed on the inner side and thus appear transversely striped; they coalesce at their base into a continuous membrane. Two cilia of the inner peristome are always situated between each two teeth of the outer row. The teeth and cilia of the peristome are formed in this instance of thickened portions of the opposite walls of a single layer of cells next to the operculum (Fig. 478), the teeth from portions of the external wall, and the cilia from portions of the internal walls of the same layer. On the opening of the capsule the unthickened portions of this layer break away and the teeth and cilia split apart.

In the Polytrichaceae the origin of the peristome teeth follows a peculiar type; they are composed of a number of elongated entire thick-walled cells.

The structure of the peristome varies greatly within the Bryales. By its peculiar form and hygroscopic movements the peristome closes the mouth of the capsule in moist weather and causes a gradual dissemination of the spores from the capsule. In some minute Mosses (*Archidium*, *Phascum*, *Pleuridium*) the sporogonium is considerably simplified, the formation of operculum, annulus, and peristome being suppressed and the spores set free by decay of the capsule

Schistostega osmundacea, a moss living in caves, has fertile shoots, which have spirally-arranged leaves and bear stalked capsules devoid of peristomes, and also other shoots that are sterile, with two rows of leaves (Fig. 474). The protonema of this species has peculiarly constructed spherical cells, and gives out an emerald phosphorescent light owing to the rays of light passing through the chloroplasts before being reflected back.

Polytrichum commune and other related Mosses have a peculiar construction of their leaves which is an adaptation for the absorption of water and a protection against drought. The leaves, which are a number of layers thick, bear on their upper surface numerous, longitudinally-running, parallel lamellae; these consist of one layer of cells containing chlorophyll and form the assimilatory tissue of the leaf.

In the spaces between the lamellae, water is conducted and retained. In dry weather the leaf rolls up by means of a cohesion mechanism and is closely applied to the stem; in this way the delicate lamellae are protected from excessive transpiration (106b).

There are other protective arrangements against drying up, but many Mosses can endure dryness without suffering harm.

The most important generic distinctions are afforded by the form of the capsule, the characters of the peristome, the operculum, and the calyptra. The earlier division of the Bryales into two large sub groups, the Acrocarpi (with the archegonium, and consequently the sporogonium. at the end of the main stem), and the Pleurocarpi (with archegonia and sporogonium on short lateral branches), is now abandoned as unnatural. In place of it the ontogeny of the peristome is used to divide the Bryales into three groups.

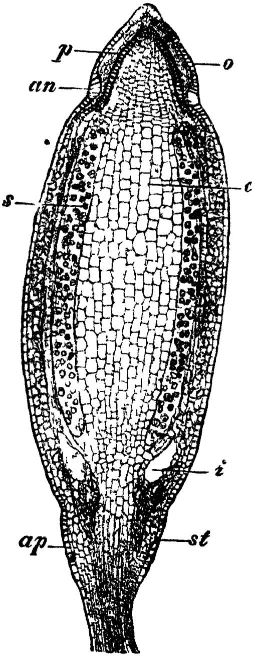


FIG. 477.—*Mnium hornum.* Median longitudinal section of a half-ripe sporogonium. *o*, Operculum; *p*, peristome; *an*, annulus; *c*, columella; *s*, spore-sac containing the spores, *i*, air space; *ap*, apophysis; *st*, stomata. (× 18. After STRASBURGER.)

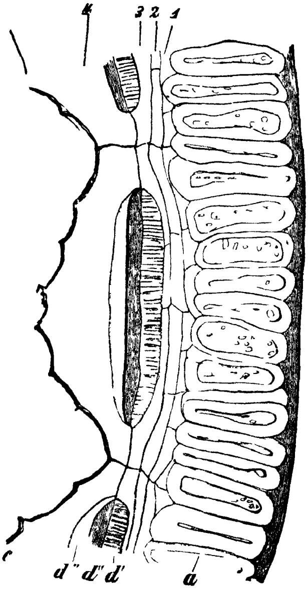


FIG. 478.—*Mnium hornum* Transverse section through the wall of the capsule in the region of the ring. *a*, Cells of the ring, *1-4*, successive cell layers with the thickened masses of the peristome, *d*, *d″*, *d″*, transverse projecting ribs; *c*, the coalesced cilia. (× 240. After STRASBURGER.)

As examples of common mosses may be mentioned *Mnium undulatum* (Fig. 475) and *M. hornum*, *Funaria hygrometrica*, *Polytrichum commune* (Fig. 473), and members of the Families Neckeraceae and Hypnaceae. *Fontinalis antipyretica* occurs submerged in streams.

Survey of the Bryophyta

The life-history of the Bryophytes is characterised by a clear ALTERNATION OF GENERATIONS. The GAMETOPHYTE is the haploid plant (including the protonema), and bears the sexual organs—antheridia and archegonia. From the fertilised egg-cell the diploid SPOROPHYTE develops and this stage ends with the asexual spores, in the formation of which the reduction-division occurs. The asexual generation does not become an independently living plant, but remains throughout its life attached to the gametophyte and nourished by it (Fig. 481).

The alternation of generations is not necessarily connected with the alternation in the nuclear phases; this has already been seen from certain facts to be the case in the Algae. In the Mosses cut-up setae can be induced to exhibit regeneration; the pieces do not, however, form a new sporogonium, but grow out to form a gametophyte which, like the sporophyte, is diploid. Fertilisation of the diploid egg-cells of such gametophytes, by their diploid spermatozoids, results in tetraploid sporogonia. The study of these has enabled investigators, especially F. von Wettstein, to draw important and interesting conclusions.

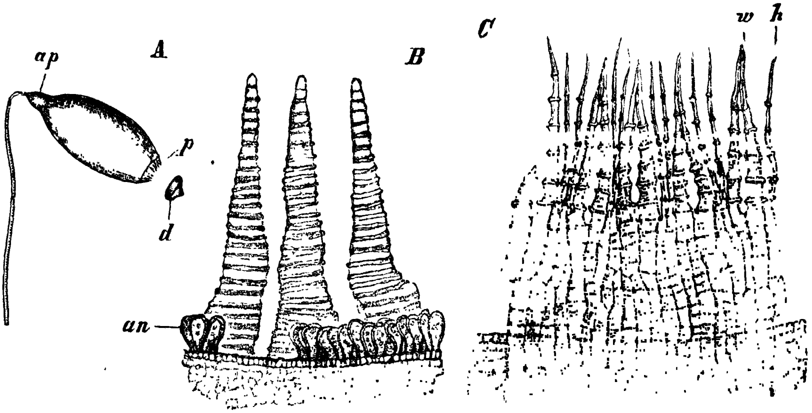


Fig. 479.—*Mnium hornum.* *A*, Capsule with upper portion of seta; *ap*, apophysis; *p*, peristome; *d*, the separated operculum. *B*, Three teeth of the outer peristome seen from the outside; *an*, annulus. *C*, Inner peristome seen from the inside; *w*, broader cilia; *h*, narrower cilia. (*A* × 4; *B*, *C* × 60.)

There are difficulties in deriving the Bryophyta phylogenetically from any particular group of Algae. No intermediate forms are known between the Bryophyta on the one hand and the higher Green Algae and the Characeae on the other.

It seems possible that the antheridia of Bryophyta may have been derived from multicellular gametangia (98) similar to those that occur in the Brown Algae. It is, however, improbable that the green Bryophyta have originated from the brown Phaeophyceae. The origin of the Archegoniatae is thus still enveloped in complete darkness.

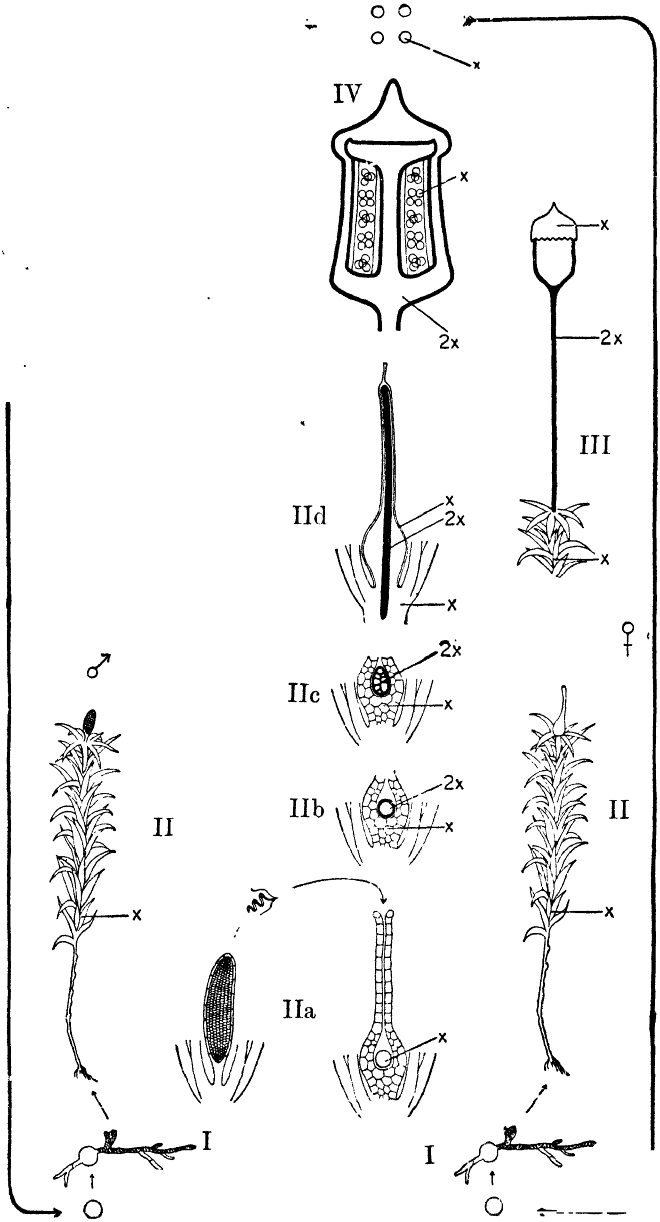


FIG. 481.—Diagrammatic representation of the development of a Moss. I. Spore and protonema; II. gametophyte, fertilisation and development of the spórophyte; III. mature sporophyte; IV. spore-formation in the capsule. *x*, haploid (thin lines), 2*x* diploid (thick lines).

With the exception of a few forms which have assumed an aquatic life, the Bryophyta are land-plants, and this is confirmed by the features of their habit. Besides primitive forms with a lobed creeping thallus there are many that have an erect stem bearing leaves, a construction that makes better use of the space and light available. Even the thalloid forms exhibit differentiation into assimilatory and storage tissues and some have stomata, serving for gaseous exchanges. In correspondence with the terrestrial life all the subaerial parts of Bryophyta are covered with a cuticle. In some species, externally differentiated into stem and leaves, conduction of materials in the plant is effected by a very simple conducting bundle composed of elongated living and dead cells, but containing neither true vessels nor sieve-tubes. Since true roots are also completely wanting, and only rhizoids are present, the Bryophyta, in spite of their high external differentiation in some respects, are not cormophytes, but thallus-plants. Their relatively small size (the largest Moss, *Dawsonia*, from New Zealand, is fifty centimetres high), is connected with the above noted features; the difficulties of providing a supply of water in large land-plants require a much more complicated structure than is found in large aquatic plants.

The two Classes of Bryophyta may be briefly characterised:

1. **Hepaticae**, Liverworts. Sexual generation with a poorly developed protonema, which is usually not sharply marked off from the thallus. The latter is either flattened and dichotomous, or is segmented into a stem bearing dorsiventrally arranged leaves. The capsule in almost all cases contains elaters as well as spores. Only in one order, the Anthocerotales, is a columella differentiated in the capsule. The spermatozoids are chemotactically attracted by protein substances.

Key to the Orders of Hepaticae:

Anthocerotales: Thallus without leaves; sporogonium with columella.

Marchantiales: Thallus without leaves; sporogonium without columella opening by an annular split or with numerous teeth.

Jungermanniales: Thallus without leaves, or leafy; sporogonium without columella, dehiscing by four lobes.

2. **Musci**, Mosses. The protonema of the sexual generation is usually strongly developed and sharply defined from the thallus, which is always segmented into stem and leaves. The leaves are spirally arranged, in many orthostichies, less commonly in two ranks; the stems are thus poly- or bi-symmetrical as regards the arrangement of their leaves. Capsule always without elaters, but with a columella. The spermatozoids react to cane-sugar. The sporogonium is usually covered by a calyptra.

Key to the Orders of Musci:

Sphagnales: Protonema, a flat thalloid structure; sporogonium spherical, borne on a pseudopodium; columella overarched by the spore-sac; capsule opening by an operculum.

Andreaeales: Protonema filamentous or ribbon-shaped; sporogonium elongated, borne on a pseudopodium; columella overarched by the spore-sac; capsule opening by longitudinal splits.

Bryales: Protonema filamentous; sporogonium with a true seta; columella continuing up to the operculum and surrounded by the cylindrical spore-sac; capsule opening by means of operculum and peristome; calyptra well-developed.

Fossil Bryophyta.—The Liverworts are more primitive in their organisation than the Mosses and appear to be more ancient, since their fossil remains are occasionally met with back to the Carboniferous period, while the earliest known Mosses are from the Upper Cretaceous. Most fossil Bryophytes are from the Tertiary rocks and closely resemble existing forms.

III. PTERIDOPHYTA (VASCULAR CRYPTOGAMS) (1, 92, 112-131)

The Pteridophytes include the Ferns, Water-Ferns, Horse-tails, and Club Mosses, as well as a number of extinct classes, and represent the most highly developed Cryptogams (for a survey see p. 542).

In the development of the plants forming this group, as in the Bryophyta, a distinct alternation of generations is exhibited (Fig. 530, p. 541).

The SEXUAL GENERATION, which here, as in the Bryophyta, is haploid, is termed the PROTHALLIUM or GAMETOPHYTE. It never reaches any great size, being at most a few centimetres in length ; in some forms it resembles in appearance a simple, thalloid Liverwort; it then consists of a small green thallus, attached to the soil by rhizoids springing from the under side (Fig. 482 *A*). On the prothallia arise the sexual organs, ANTHERIDIA (Figs. 509, 516), producing numerous, and usually spiral, spermatozoids, which are multiciliate or biciliate, and ARCHEGONIA (Figs. 510, 517), in each of which is a single egg-cell. As in the Mosses, the presence of water is necessary for fertilisation. The spermatozoids are induced to direct their motion toward the archegonia by the excretion from the latter of a substance which diffuses into the surrounding water (cf. p. 332).

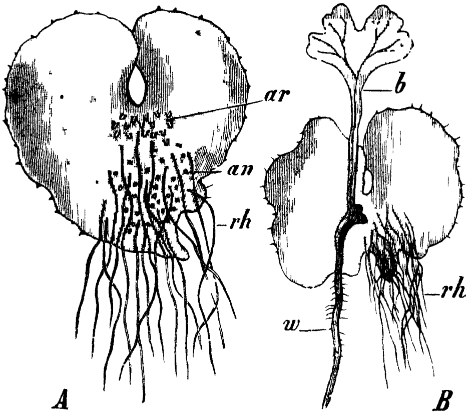


FIG 482.—*Dryopteris (Aspidium) filix mas.* *A*, Prothallium seen from below, *ar*, archegonia, *an*, antheridia; *rh*, rhizoids *B*, Prothallium with young fern attached to it by its foot, *b*, the first leaf, *w*, the primary root. (× circa 8)

The egg-cell, after its fertilisation by a spermatozoid, develops into the plant of the ASEXUAL GENERATION or SPOROPHYTE. This in the Pteridophyta is quite differently constructed, and much more highly developed, than in the Bryophyta. Resemblances to the latter are only found in the early stages of development.

The fertilised egg-cell, while still in the archegonium, surrounds itself with a cell-wall and undergoes division, first into two cells, by the formation of a basal wall, and then into octants by two walls at right angles to each other and to the basal wall. There are exceptions to this.

Further divisions of these eight cells (Fig. 483 *A*) lead to the formation of a multicellular embryo, one sector of which projects as a mass of tissue termed the foot (Fig. 483 *f*). By means of this the young plant remains fixed in the enlarging venter of the archegonium. The foot serves as an haustorial absorbent organ in the nutrition of the embryo.

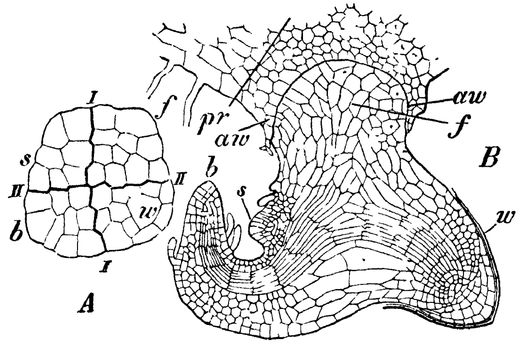


FIG. 483.—*A*, *Pteris serrulata*, embryo freed from the archegonium, in longitudinal section (after KIENITZ-GERLOFF): *I*, basal wall; *II*, transverse wall dividing the egg-cell into quadrants; rudiment of the foot *f*, of the stem *s*, of the first leaf *b*, of the root *w*. *B*, Section of a further-developed embryo of *Pteridium aquilinum* (after HOFMEISTER); *f*, foot still embedded in the enlarged venter of the archegonium *aw*; *pr*, prothallium. (Magnified.)

The further development of the sporophyte in the Pteridophyta is fundamentally different from that in the Bryophytes. From distinct sectors of the embryo, apices are differentiated which proceed to grow into the root, stem, and first leaf of the young plant (Figs. 483 *w*, *s*, *b*, 482 *B*). The prothallium usually dies after the development of the young plant (though if fertilisation is prevented it may continue to live for years) and the sporophyte becomes the independently living fern-plant. The three primary organs in most Pteridophyta grow by means of apical cells (Figs. 96, 97, 149). The stem which bears leaves is frequently dichotomously branched, the roots have a root-cap (Fig. 149), their lateral roots arising endogenously; and the leaves correspond in structure with those of the Phanerogams. Stems, leaves, and roots are traversed by well-differentiated vascular bundles, which are here first met with in the vegetable kingdom; the water-conducting elements are tracheides with scalariform thickening (Fig. 67). The bundles of the great majority of Pteridophytes are as a rule constructed on the concentric and radial types (cf pp. 95 ff, Figs 484, 485) Secondary growth in thickness, resulting from the activity of a special cambium, occurs only occasionally in existing forms, but it was characteristic of the stems of certain extinct groups of Pteridophytes

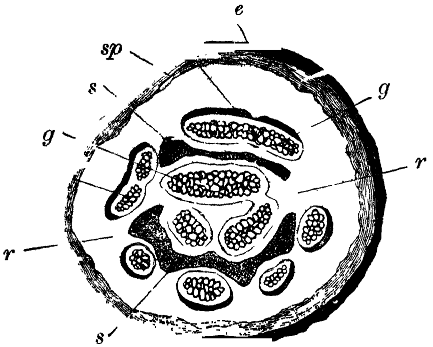


FIG 484 —Transverse section of the rhizome of *Pteridium aquilinum* *g* Concentric vascular bundles *s*, sclerenchymatous plates *p* peripheral zone of sclerenchymatous fibres, *r*, cortex *e* epidermis (× 7)

The sporophyte is thus a true CORMUS and the Pteridophyta are the earliest members of the phylogenetic tree which do not belong to the thalloid plants

The SPORES are produced in special receptacles termed SPORANGIA (Fig 486), which occur on the asexual generation,

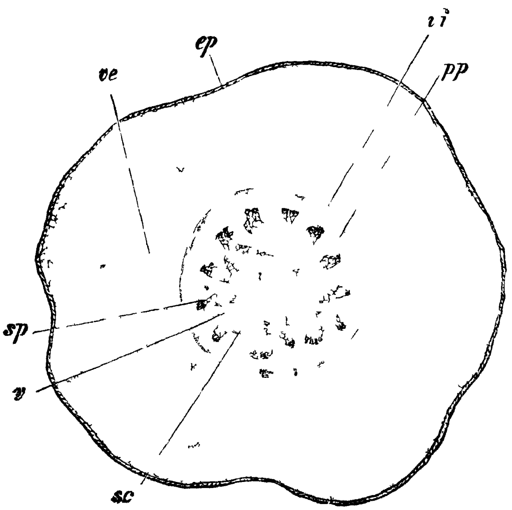


FIG 485 —Transverse section of stem of *Lycopodium complanatum* *ep* Epidermis *ve ri pp* outer, inner, and innermost parts of the primary cortex, surrounding the central cylinder composed of xylem and phloem regions *sc*, scalariform tracheides *sp* annular and spiral tracheides, *v*, phloem (× 26 After STRASBURGER)

either on the leaves, or less frequently on the stems in the axils of the leaves The leaves which bear the sporangia are termed SPOROPHYLLS. The sporophylls are frequently of simpler form than the assimilatory leaves, and are associated in special shoots, which may be termed flowers.

The sporangium consists of a wall enclosing the sporogenous tissue, the cells of which, becoming rounded off and separated from each other as spore-mother-cells, give rise each by a reduction-division to four tetrahedral spores (spore-tetrads). The cells of the innermost layer of the sporangial wall are rich in protoplasm, and constitute the TAPETUM. In the course of the development of the sporangium the tapetal cells wander in between the spore-mother-cells, their nuclei dividing amitotically, so that the spores eventually lie embedded in a mucilaginous protoplasmic mass, the PERIPLASMODIUM, from which they derive nourishment (114). The periplasmodium is used up in the formation of the walls of the spores. The young spore on becoming isolated in the tetrad surrounds itself with a cutinised membrane (exospore) within which a cellulose layer (endospore) is deposited. In many cases a perispore is deposited by the periplasmodium upon the exospore.

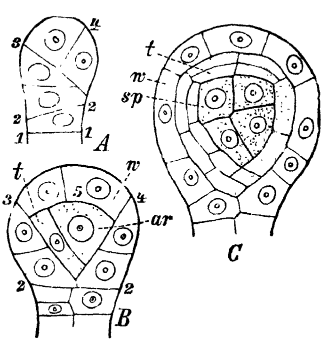


FIG. 486.—Development of the sporangium of *Asplenium*. *A*, First divisions of the young sporangium which has originated from a single superficial cell. *B*, Division into the wall (*w*), and the central archesporial cell (*ar*) which has cut off one of the tapetal cells (*t*). *C*, Older stage in which the archesporial cell has given rise to the tapetal cells and the sporogenous tissue (*sp*). (× 300. After SADEBECK.)

The spores of the majority of the Pteridophytes are of one kind, and give rise on germination to a prothallium, which produces both antheridia and archegonia. In certain cases, however, the prothallia are dioecious. This separation of the sexes extends in some groups even to the spores, which, as MACROSPORES (megaspores), developed in MACROSPORANGIA (megasporangia), give rise only to female prothallia; or as MICROSPORES, which are produced in MICROSPORANGIA, develop similarly only male prothallia. In accordance with this difference in the spores, a distinction may be made between the HOMOSPOROUS and HETEROSPOROUS forms of the same group; but this distinction has no systematic value in defining the different groups themselves, as it has arisen independently in several of them.

A survey of the Classes of Pteridophyta is given on p. 542.

CLASS I

Psilophytinae (135)

The Psilophytinae are only known as fossils from the Devonian rocks. They were plants of small size, and are the most primitive Pteridophytes known.

Rhynia (Fig. 487) had no true roots but subterranean rhizomes; there was a true vascular bundle in the leafless, dichotomously-branched, assimilatory axes.

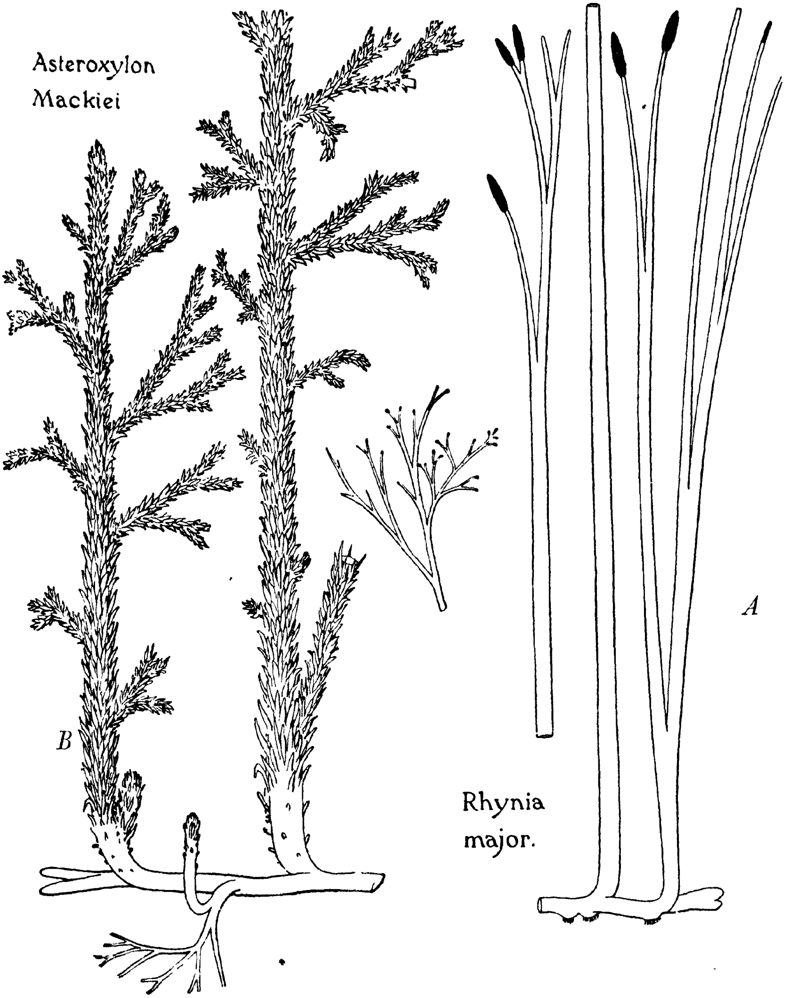


FIG. 487.—*A*. Restoration of *Rhynia major*, showing the rhizome bearing rhizoids, the dichotomously-branched leafless axes, and the large terminal sporangia. *B*. Restoration of *Asteroxylon Mackiei*, showing the leafless rhizomes and the branched sub-aerial stems clothed with small leaves. The detached leafless branch-system with small terminal sporangia is probably the fertile portion of the plant, but has not been found in connection with the leafy shoots. (Reduced; after KIDSTON and LANG.)

In *Asteroxylon* the stems were closely covered by small leaves a few millimetres in length. The sporangia were terminal on the axes without any relation to leaves and had a wall composed of several layers of cells. They were filled with spores formed in tetrads. In the case of *Hornea* (Rhyniaceae) there was a column of sterile tissue within the sporangium resembling the columella of some Mosses.

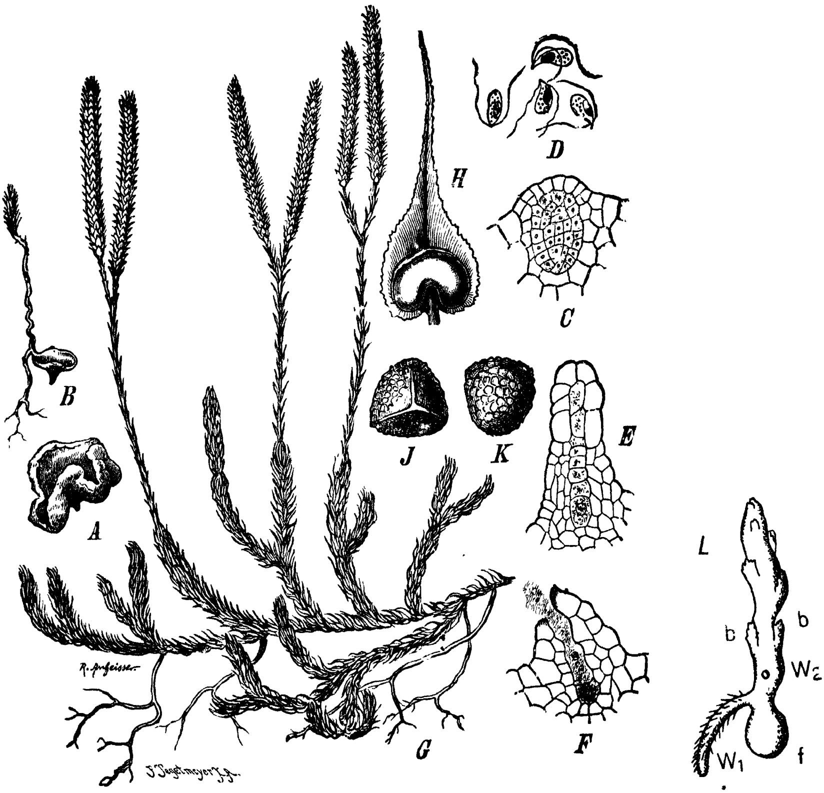


FIG. 488.—*Lycopodium clavatum*. *A*, Old prothallus. *B*, Prothallus with young plant attached. *C*, Antheridium in vertical section. *D*, Spermatozoids. *E*, Young archegonium, the neck still closed. *F*, Open archegonium ready for fertilisation. *G*, Plant bearing cones (½ nat. size). *H*, Sporophyll with an opened sporangium. *J*, *K*, Spores from two points of view. *L*, A young subterranean sporeling still without chlorophyll (× 7); *f*, foot; *w*, root; *b*, scale-leaves. (*A*-*F* and *L* after BRUCHMANN.)

CLASS II

Lycopodiinae (Club-Mosses) (1, 92, 112, 115, 125-129, 132, 133)

Order 1. Lycopodiales (125)

The numerous widely-distributed species of the genus *Lycopodium* (Club Moss) are for the most part terrestrial plants; in the tropics many pendulous epiphytic forms also occur. In *Lycopodium clavatum*, one of the commonest of our native species, the stem, which is thickly covered with small, awl-shaped leaves, creeps along the ground; it branches dichotomously, and gives rise to ascending lateral branches, while from the under side spring the dichotomously-branched roots (Fig. 488). The cones, consisting of the closely-aggregated sporophylls, are situated in groups of two or more at the ends of the forked erect shoots. The sporophylls are broader and more prolonged at the tip than the sterile leaves; each bears a large reniform sporangium on the upper side at the base. The sporangium opens into two valves and sets free numerous minute spores (Fig. 488 *H*). The spores are all of one kind, and in consequence of their formation in tetrads are of a tetrahedral though somewhat rounded shape. The exospore is covered with a reticulate thickening (Fig. 488 *J*, *K*).

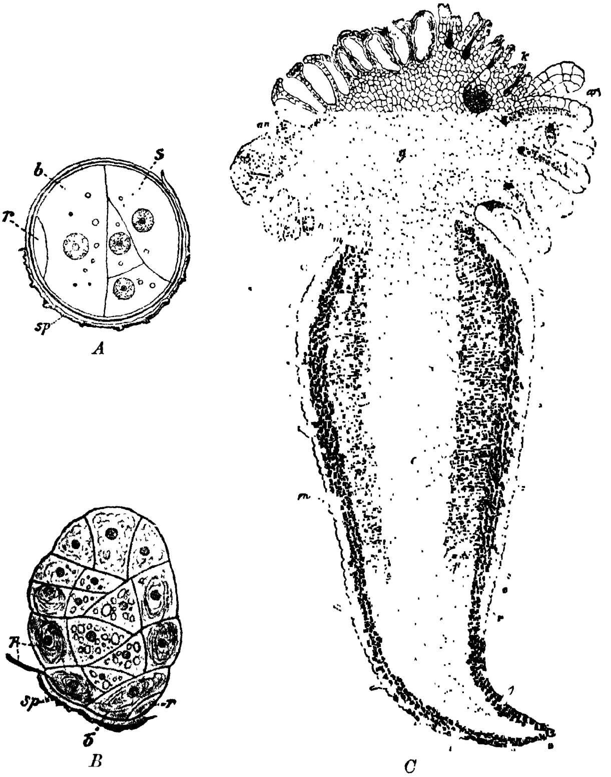


Fig. 489.—*A*, Germinating spore of *Lycopodium annotinum*; *r*, rhizoid cell; *b*, basal cell; *s*, apical cell; *sp*, spore-membrane (× 580). *B*, Older stage of the prothallus of the same species, showing the endophytic fungus (*p*) in the lower cells, and the apical cell divided into three meristematic cells (× 470). *C*, *Lycopodium complanatum*. Prothallus with antheridia (*an*), archegonia (*ar*), and a young embryo (*k*) (× 26). (After Bruchmann.)

The spores only germinate after six to seven years, forming at the expense of their reserve materials a prothallus of five cells. Further development only takes place when fungal hyphae enter the lowest cells (Fig. 489 *A*, *B*). The prothallia of *Lycopodium clavatum* (Fig. 488 *A*, *B*) are small, white, tuberous structures, which live as subterranean saprophytes. At first top-shaped, they become converted by the continued marginal growth into cup-shaped lobed bodies which may attain a size of two centimetres. Long rhizoids spring from the lower surface, while the upper surface bears numerous antheridia and archegonia. The endophytic fungus is confined to the peripheral tissues of older prothalli; it may emerge through the specialised basal cells of the rhizoids and invest the latter (125a). Only after twelve to fifteen years is the prothallus sexually mature, so that its life may last some twenty years. In other species of *Lycopodium* the prothalli are turnip-shaped, cylindrical or conical; they always harbour an endophytic fungus, forming a mycorrhiza. In some species they project above the surface of the soil and are of a green colour.

The prothallia are monoecious and bear the sexual organs on their upper portion. The antheridia are somewhat sunk in the tissue (Fig. 488 *C*) and enclose numerous spermatozoid-mother-cells, in which small oval spermatozoids (*D*), with two cilia attached below the apex, are formed. The archegonia (Fig. 488 *E*, *F*) have often numerous neck-canal cells (up to twenty), but these may be reduced to one, as in *L. cernuum*. The upper cells of the neck become disorganised on opening.

The embryo (Fig. 490) remains during its development enclosed in the prothallus into which it is forced by the suspensor (Fig. 490 *et*) which develops on the side turned towards the archegonial neck. Beneath the foot the young shoot forms; the first leaves are scale-like, and from the basal portion of the shoot the first root develops. There are no definite apical cells.

The spores of *Lycopodium clavatum* and other species are sometimes used in pharmacy.

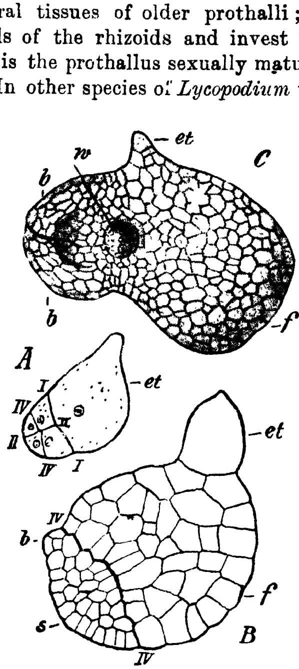


FIG. 490.—Development of the embryo in *Lycopodium complanatum*. *A*, Embryo showing the first divisions; the basal wall *I* separates the suspensor (*et*) from the body of the embryo; the transversal walls *II* and *III* (the latter being in the plane of the section) together with the transverse wall *IV* give rise to two tiers of four cells; the tier next the suspensor gives rise to the foot, the terminal tier forms the shoot (× 112). *B*, Embryo of medium age; *s*, apex of stem; *b*, rudiment of leaf; *f*, foot (× 112). *C*, Embryo shortly before breaking out of the prothallus; *bb*, the two first leaves covering the apex of the stem; *w*, the first root (× 40). (After BRUCHMANN.)

Order 2. Selaginellales (126)

To this order belongs the genus *Selaginella*, represented by numerous and for the most part tropical species. They have, as a rule, profusely-forked, creeping, and sympodially-branched stems, but occasionally erect, branched stems; some form moss-like beds of vegetation; others, climbing on adjacent plants, possess stems several metres long. Certain xerophytic species (*S. lepidophylla* in tropical America, etc.) can endure drying up for months or even years, closing together their rosette-shaped shoots by a cohesion-mechanism, and expand again on the arrival of rain (127). In general the Selaginellas are similar in habit to the Lycopodiums. They have small scale-like leaves which usually exhibit a dorsiventral arrangement, such as is shown, for example, in the alpine *Selaginella helvetica* (Fig. 491), the stem of which bears two rows of small, dorsal, or upper leaves, and opposite to them two rows of larger, ventral, or under leaves. (Cf. also Fig. 137.) In plagiotropous forms, completely leafless lateral shoots, the RHIZOPHORES ([128]) are usually present. They grow towards the soil owing to positive geotropism, and there produce endogenous roots from their tips. The leaves of *Selaginella* are characterised by the presence at their base on the upper side of a small membranous LIGULE. This serves as an organ for the rapid absorption of water (rain-drops) by the leafy shoot ([129]).

The CONES or flowers (Fig. 492) are terminal, simple or branched, radially symmetrical, or less commonly dorsiventral. Each sporophyll subtends only one sporangium, which springs from the stem above the leaf-axil. The spores differ in size, there being macrospores and microspores. The same spike bears both macrosporangia and microsporangia. Each MACROSPORANGIUM (Fig. 492 *A*, *C*) contains only four macrospores, which are produced by the growth and division of a single spore-mother-cell; all the other mother-cells originally developed ultimately disappear. On account of the increasing size of the spores the spherical macrosporangia become nodular. Numerous spores are formed in the flattened MICROSPORANGIA. Opening, which is due to a cohesion-mechanism, occurs along definite lines of dehiscence.

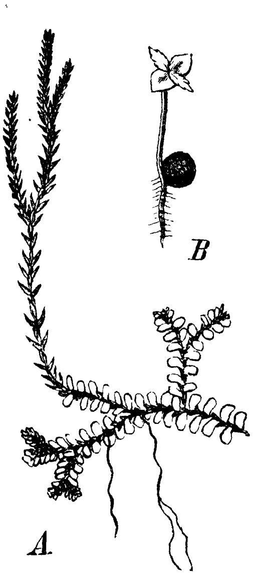


FIG. 491.—*A*, *Selaginella helvetica* (from Nature, nat. size). *B*, *Selaginella Kraussiana*, embryonic plant with macrospore still attached. (After BISCHOFF, magnified.)

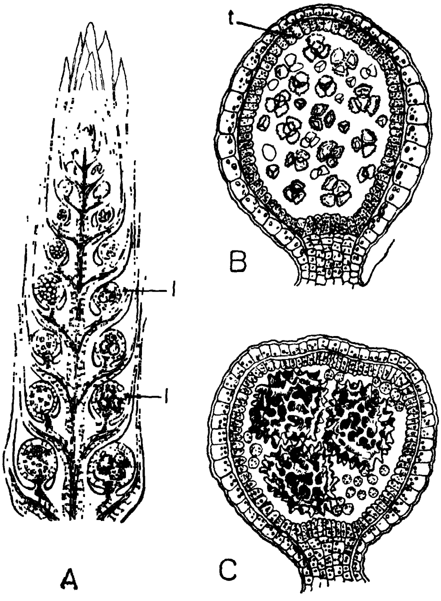


FIG. 492.—*Selaginella inaequalifolia*. *A*, longitudinal section of a cone showing to the left microsporangia and to the right macrosporangia. *B*, microsporangium containing tetrads of microspores. *C*, macrosporangium with one tetrad of macrospores. *t*, tapetal cells, *l*, ligule. (*B* and *C* × 70. After SACHS.)

The microspores begin their development while still enclosed within the sporangium. The spore first divides to separate a small lenticular vegetative cell from a large cell, which divides successively into eight sterile prothallial or wall-cells and two or four central spermatogenous cells (Fig. 493 *A*). These cells represent the greatly reduced prothallus which is formed within the spore. Only the small lens-shaped cell is to be regarded as vegetative; it is termed the rhizoid-cell. The remaining cells represent a single antheridium. By the further division of the central cells of this numerous spermatozoid mother-cells are formed (*B-D*). The peripheral cells then break down and give rise to a mucilaginous substance, in which is embedded the central mass of spermatozoid mother-cells (*E*). The small prothallial cell (*p*), however, persists. The whole male prothallium is up to this stage still enclosed by the wall of the microspore. This ultimately ruptures, and the mother-cells are set free and liberate the club-shaped spermatozoids. Each of these has two long cilia at its pointed end.

The less reduced female prothallus is formed from the macrospore (Fig. 494). The nucleus of the spore forms many daughter-nuclei which are distributed in the protoplasm lining the wall, especially at the apex of the spore. The formation of cell-walls then takes place, proceeding from the apex to the base till the whole spore is filled with larger prothallial cells; a further division into smaller cells proceeds in the same direction. In this small-celled tissue at the summit of the prothallus a few archegonia are developed.

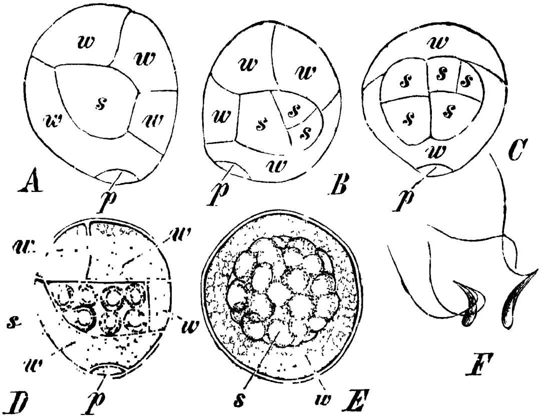


FIG. 493.—*A-E*, *Selaginella stolonifera*, successive stages in the germination of a microspore; *p*, prothallial cell; *w*, wall-cells of antheridium; *s*, spermatogenous cells; *A*, *B*, *D*, lateral, *C*, dorsal view. In *E* the prothallial cell is not visible, the disorganised wall-cells enclose the spermatozoid mother-cells; *F*, spermatozoids of *Selaginella cuspidata*. (*A-E* × 640, *F* × 780. After BELAJEFF.)

The wall of the spore eventually bursts at the apex, and the prothallium becomes partially protruded; it forms a number of rhizoids on three projections of its tissue, and these assist the bursting of the spore-wall and also hold water. The fertilisation of one or two archegonia, which then takes place, is followed directly by the segmentation of the fertilised egg-cells and the formation of the embryos (Fig. 494).

The development of the embryo, in which a suspensor consisting of one or several cells, the apex of the stem with the first leaves, the first rhizophore and the foot are distinguishable, proceeds in a great variety of ways in the genus. The first division in the fertilised egg-cell is transverse. In *S. Martensii*, and related forms, the upper hypobasal cell gives rise to the suspensor only, the main portion of the embryo being derived from the lower cells (Fig. 495); in

most other species the upper cell forms the foot and rhizophore as well as the suspensor. The apex of the shoot with the first pair of leaves grows upwards

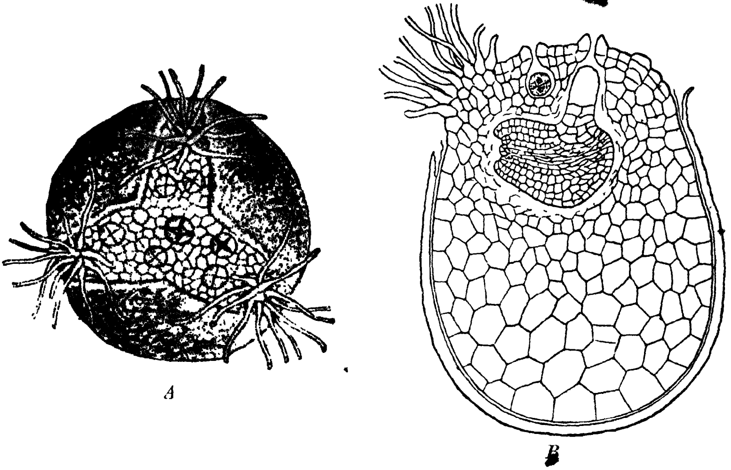


FIG. 494.—*Selaginella Martensii* *A*, Ruptured macrospore seen from above, showing the prothallus with three groups of rhizoids and several archegonia (× 112) *B*, Longitudinal section of the prothallus showing two archegonia in which embryos are developing (× 112). (After BRUCHMANN.)

and the root downwards; the young plant remains attached to the prothallus in the megaspore by the foot (Fig 491 *B*).

In some species the female prothallus is developed in the macrospores while they are still within the macrosporangium; even fertilisation may take place in the sporangium. In the latter case the microspores, containing already free spermatozoids, reach the opened macrospores; the microspore then opens and the spermatozoids swim to the archegonia. In *S. rupestris* the macrospore remains in the sporangium, so that the development of the young plant (the sporophyte) takes place on the sporophyte of the preceding generation.

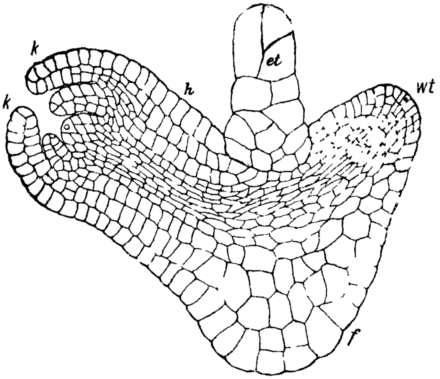


FIG. 495.—*Selaginella Martensii* Embryo before becoming free from the prothallus in longitudinal section; *f*, foot; *wt*, rhizophore, *et*, suspensor; *k*, cotyledons with their ligules. (× 150. After BRUCHMANN)

Order 3. Lepidodendrales (132, 133)

The extinct Lepidodendrales which lived in the Devonian, Carboniferous and Permian periods formed trees with secondary thickening, that sometimes attained a height of 30 m. (Fig. 496). The stems were closely covered with simple, narrow leaves, which, though they may be 15 cm. long, can be regarded as small relatively to the stem. There was a ligule at the base of each leaf, and the leaf was traversed by a single vascular bundle. When the leaves were shed, characteristic scars were left on the surface of the stem.

In the **Lepidodendraceae** the spirally arranged leaves were seated on rhombic leaf-cushions (Fig. 496, 2). The stems were dichotomously branched, and the cones (flowers) terminated some of the branches (Fig. 496, 1). The Lepidodendraceae were heterosporous (Fig. 497), and developed prothalli which resembled those of the Selaginellaceae.

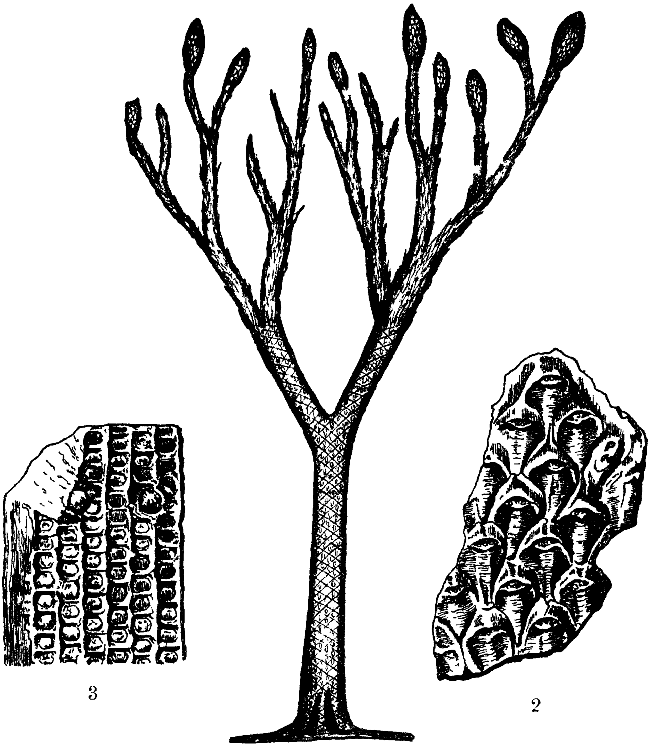


FIG. 496.—*1, Lepidodendron.* Reconstruction (after POTONIE). *2, Lepidodendron,* leaf-cushions. *3, Sigillaria,* leaf-scars. (From LOTSY and WETTSTEIN.)

The **Sigillariaceae** had columnar, unbranched, or sparingly dichotomous stems which were clothed with longitudinal rows of more or less hexagonal leaf-scars (Fig. 497, 3). The cones, which were similar to those of the Lepidodendraceae, were borne on the stems.

Some palaeozoic Lepidodendrales (*Lepidocarpon, Miadesmia*) are of special interest since they bore seed-like structures; they may therefore be grouped together as the Lepidospermae. The macrosporangium was surrounded by an outgrowth from the sporophyll, which formed an integument-like structure with

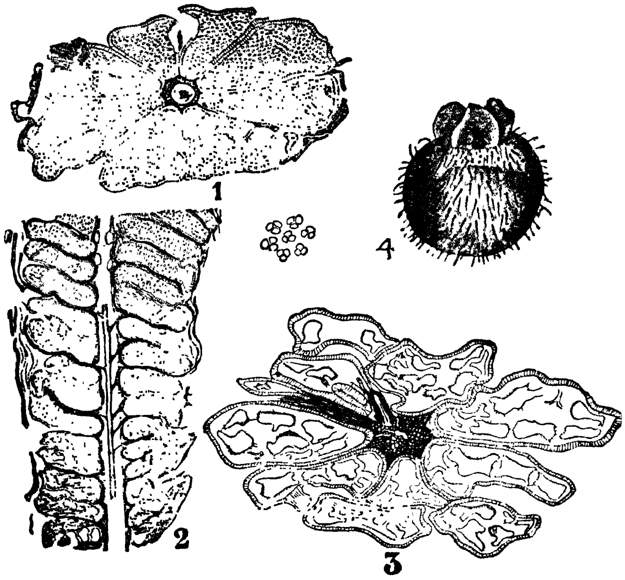


FIG. 497.—*Lepidostrobus Veltheimianus*. *1*, Transverse section of cone with microsporangia; tetrads to right below. *2*, Cone in longitudinal section showing microsporangia above and macrosporangia below. *3*, Transverse section of cone with macrosporangia. *4*, Macrospore, probably opening in course of germination. (After SCOTT, KIDSTON, BINNEY.) From LOTSY.

an opening along its summit (Fig. 498). Only one macrospore attained full development; the prothallus remained enclosed by the wall of the spore. Probably the microspores reached the macrosporangia while the latter were still attached to the parent-plant; later the macrosporophylls with their sporangia became free. Similar relations will be met with in the Gymnosperms.

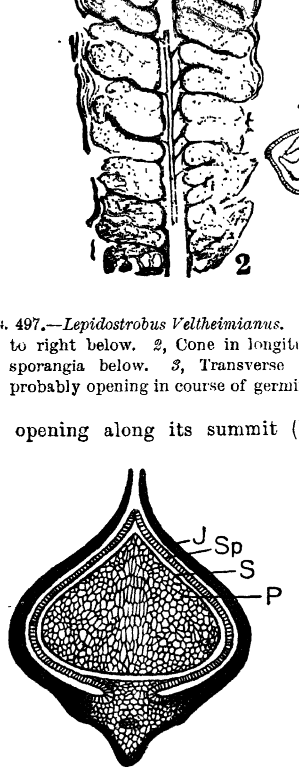


FIG. 498.—*Lepidocarpon Lomaxi*. Diagrammatic section across a macrosporangium with prothallus, P; spore-wall, S; sporangial wall, Sp; integument, J. (After SCOTT from WETTSTEIN.)

The dichotomous branching of the root and stem, and the simple form of the numerous small leaves are characteristic of all Lycopodiinae. The leaves are closely placed, so that the stem does not appear segmented into internodes. The sporophylls differ little in form from the assimilatory leaves, and are grouped as cones at the ends of certain shoots. A single sporangium is borne on the upper side of the sporophyll near its base. The innermost layer of the wall, forming the tapetum, is not broken down when the sporangium is mature. The spermatozoids, unlike those of all other Pteridophytes, are biciliate. The embryo is carried down into the tissue of the prothallus by means of a suspensor.

The three orders are distinguished by the following characters:

Lycopodiales: Isosporous herbs, with, for the most part, subterranean prothalli depending for their saprophytic nutrition on an endophytic fungus. Leaves without ligule.

Selaginellales: Heterosporous herbs with extremely reduced, dioecious prothalli, which are developed within the spores. Fertilisation sometimes taking place on the parent-sporophyte. Leaves with ligule.

Lepidodendrales: Extinct trees with secondary growth in thickness. Heterospory and development of the prothalli as in the Selaginellales. In the most highly developed forms the macrospore was invested by an integument, and fertilisation probably took place on the parent-plant. Leaves with ligule.

The most ancient Lycopodiinae are those known from the Devonian. The group was represented by numerous dendroid forms in the Carboniferous period, and was then more highly developed than at the present day.

CLASS III

Psilotinae (130)

This class is apparently a survival; the existing forms are only *Psilotum* with two tropical species and *Tmesipteris* with one Australasian species. The total absence of roots is noteworthy. The dichotomously branched stems bear small, simple leaves, spirally arranged. The sporophylls in the upper regions of the shoots are always deeply bifid; each bears near the base of its upper side a thick-walled bilocular or trilocular sporangium. Isosporous.

The prothalli of both genera are only a few millimetres long, and occur in the substratum. They are cylindrical, branched, colourless thalli harbouring a phycomycetous mycelium as a mycorrhiza. Numerous archegonia and antheridia are developed on them. The spermatozoids are multiciliate, a point of contrast with the Lycopodiinae, and of agreement with the other Pteridophyta.

CLASS IV

Equisetinae (Horse-tails) (1, 92, 112, 113, 124, 132)

Order 1. Equisetales

The only existing **Family** is the **Equisetaceae**, including the one genus *Equisetum*, comprising 20 species, found widely distributed over the whole world. The genus can be traced back to the Triassic period. Developed partly as land-, partly as swamp-plants, they may always be distinguished by the characteristic structure and habit of the asexual generation. They have a branching, underground rhizome on which arise erect, aerial haulms, usually of annual growth. The aerial haulms either remain simple, or they give rise to branch-whorls, and these in turn to whorls of a higher order. All the axes are formed of elongated internodes; they have a central pith-cavity and a peripheral series of smaller air channels. The collateral vascular bundles form a single circle, as seen in transverse section (Fig. 499). At each node is borne a whorl of scale-leaves pointed at the tips, and united below into a sheath closely enveloping the base of the internode. There is a single vascular bundle in each leaf. The lateral branches are developed in the axils of the scale-leaves, but, not having space to grow upwards, they pierce the narrow sheath. As a result of the reduction of the leaf laminae, the haulms themselves assume the function of assimilation, and for that purpose their cortical tissue under the epidermis is provided with chlorophyll. The rhizome of the common Horse-tail, *Equisetum arvense*, and that of other species, develop also short tuber-like branches which serve as reservoirs of reserve-material and hibernating organs (Fig. 500).

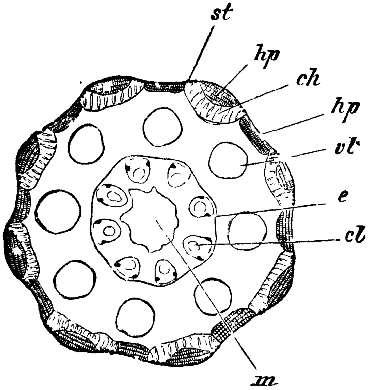


FIG. 499.—*Equisetum arvense*. Transverse section through the stem. *m*. Lysigenic medullary cavity; *e*, endodermis; *cl*, carinal canals in the collateral bundles; *vl*, vallecular cavities; *hp*, sclerenchymatous strands in the furrows and ridges; *ch*, tissue of the primary cortex containing chlorophyll; *st*, rows of stomata. (× 11. After STRASBURGER.)

The SPORANGIA are borne on specially shaped leaves or sporophylls. The sporophylls are developed in whorls, but are closely aggregated at the tips of the erect fertile shoots into a cone (flower) (Fig. 500). The lowest whorl is sterile, and forms a collar-like protuberance. The sporophylls (Fig. 500 *B*, *C*) are stalked and have a peltate expansion, on the under side of which are borne the (5-10) sac-like sporangia. In the young sporangium the sporogenous tissue is surrounded by a wall consisting of several cell-layers, but eventually the tapetal cells of the inner layer become disorganised, and their protoplasm penetrates between the developing spores, forming the periplasmodium. At maturity the wall of the sporangium consists only of the outermost of the original layers; the cells of this are provided with annular and spiral thickenings. The sporangia thus resemble the homologous pollen-sacs of Phanerogams. The dehiscence is determined by the cohesive force of the diminishing amount of water in the cells of the outer layer and the contraction of the thin parts of the cell-walls on drying. The sporangia split longitudinally, and set free a large number of green spores, which are nearly spherical in shape, and have peculiarly constructed walls. In addition to the endospore and exospore, the spores are overlaid with a perispore deposited by the periplasmodium, and consisting of two spiral bands (elaters) which are attached to the spores only at their point of intersection (Fig. 500 *D*, *E*). On drying, the spiral bands loosen and become uncoiled; when moistened, they close again around the spore. By means of their hygroscopic movements they serve to hook together the spores, and in this way ensure the close proximity of the prothallia, which are usually dioecious.

The spores are all of one kind, and on germination give rise to thalloid, green PROTHALLIA (Fig. 501). In order to form female organs the nutrition must be good; poorly nourished prothallia bear antheridia only. The female prothallia are larger than the male, and, branching profusely, are covered on the upper surface by erect lobes at whose base the archegonia are produced. The spermatozoids,

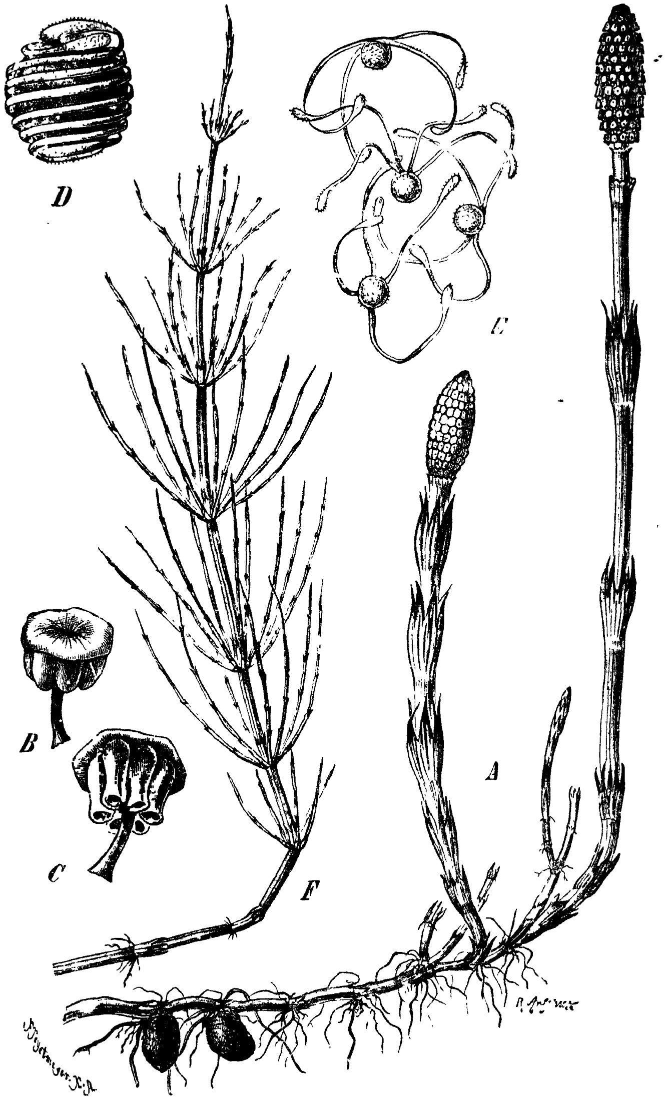


FIG. 500.—*Equisetum arvense.* *A*, Fertile shoots, springing from the rhizome, which also bears tubers; the vegetative shoots have not yet unfolded. *F*, Sterile vegetative shoot. *B*, *C*, Sporophylls bearing sporangia, which in *C* have opened. *D*, Spore showing the two spiral bands (elaters) of the perispore. *E*, Dry spores showing the expanded spiral bands. (*A*, *F*, ½ nat. size. *B*, *C*, *D*, *E*, enlarged.)

bear numerous cilia (Fig. 501 *C*). The first leaves of the embryo are arranged in a whorl and encircle the apex of the stem. *The growth of the stem is effected by the division of a three-sided apical cell (Figs. 501 IV, 96, 97).*

In certain species some of the aerial shoots always remain sterile, branching profusely, while others which produce the terminal cones either do not branch at all, or only at a later stage, and then sparingly. This distinction between the sterile and fertile shoots is most marked in *Equisetum arvense* and *Equisetum Telmateja*, in both of which the fertile shoots are entirely unbranched and terminate in a single cone (Fig. 500). They are further distinguished from the vegetative shoots by their lack of chlorophyll and their light reddish colour.

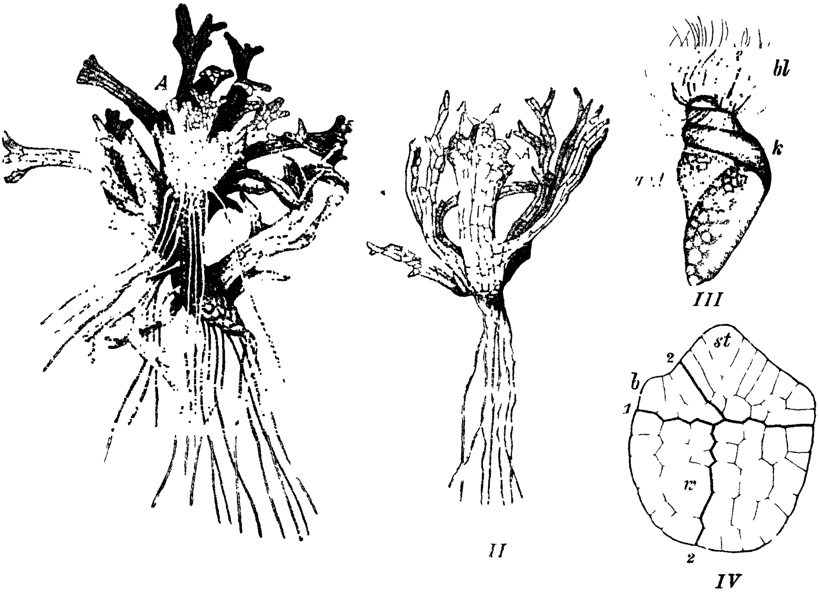


FIG. 501.—*Equisetum pratense. I*, Female prothallium from the under surface, showing the archegonia (*A*). *II*, Male prothallium with antheridia (*A*); *d*, cover cells of antheridia. (*I* × 17, *II* × 12. After GOEBEL.) *III*, *Equisetum arvense.* Spermatozoid: *k*, nucleus; *bl*, cilia-forming blepharoplast with cilia; *zyt*, cytoplasm. (× circa 1250. After SHARP.) *IV*, *Equisetum arvense.* Embryo: *1*, *2*, octant walls. The stem (*st*) and first leaf-whorl (*b*) arise from the upper half, and the root (*w*) and foot from the lower half. (× 165. After SADEBECK.)

Equisetum giganteum, growing in tropical South America, is the tallest species of the genus; its branched haulms, supported by neighbouring plants, attain a height of over twelve metres, and are about two cm. in diameter.

The outer epidermal walls of the stem are more or less strongly impregnated with silica. In *Equisetum hiemale*, and to a less degree in *Equisetum arvense*, the silicification of the external walls is carried to such an extent that they are used for scouring metal utensils and for polishing wood.

POISONOUS substances are formed in some species of *Equisetum*, and hay with which the shoots are mixed is injurious to cattle.

Family 2. Calamariaceae (132).—This extinct group was highly developed in the palaeozoic period, especially in the Carboniferous, when it was represented by numerous species. The plants resembled the Horse-tails in general habit, but in

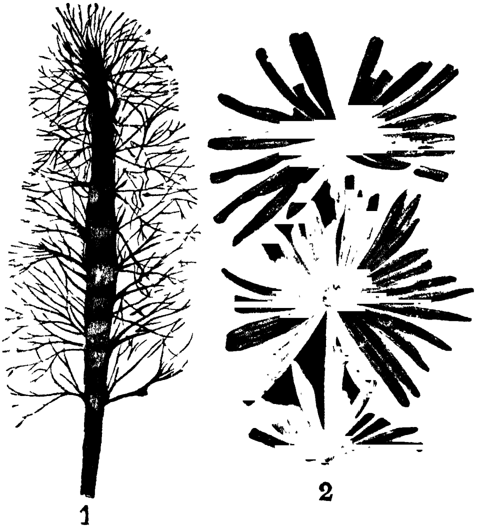


Fig 502 —*1, Asterocalamites radiatus* (After Stur) *2, Annularia stellata* (After Seward) From Lotsy, *Botan Stammesgeschichte*

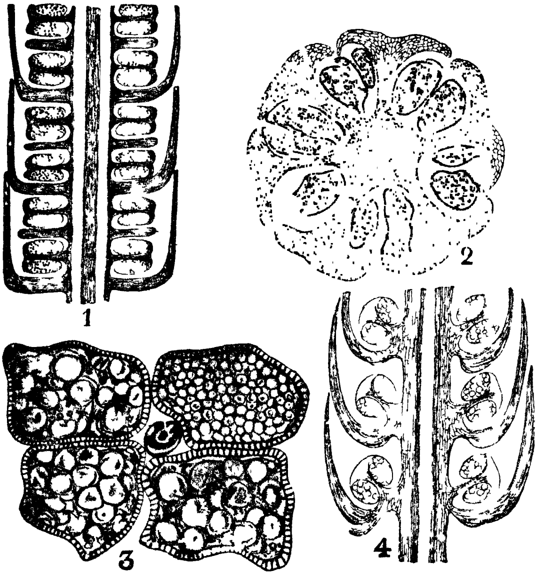


Fig 503 —*1, Calamostachys Binneyana*, Cone in longitudinal section *2*, The same in transverse section *3*, *Calamostachys Casheana*, Transverse section of a sporangiophore, showing the stalk and three macrosporangia and one microsporangium. *4*, *Palaeostachya*, Longitudinal section of cone with axillary sporangiophores. (After Scott and Hickling From Lotsy.)

some cases attained the size of trees 30 metres high; the hollow stem, which bore whorls of branches at the nodes, was covered with a periderm, and underwent secondary thickening. The leaves (Fig. 502) stood in alternating whorls; their form was narrowly lanceolate and at their bases they united into a sheath.

The cones or flowers had in *Asterocalamites* the same structure as those of *Equisetum*; in most cases they were more complicated, whorls of superposed scale-leaves separating the whorls of specialised sporangiophores. Each of the latter was a stalked peltate disc bearing, on its under side, four sporangia. It is an interesting fact that heterosporous as well as homosporous form occur among the Calamarieae. (*Calamostachys*, Fig. 503, 3).

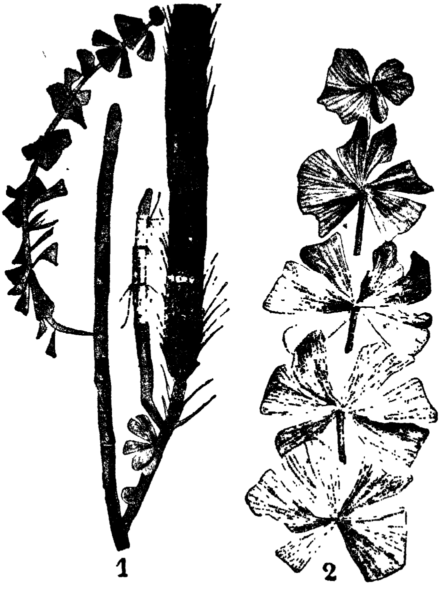


Fig. 504.—*1*, *Sphenophyllum*, showing the branched stem with both linear and wedge-shaped leaves and, on the right, an elongated cone. (After Scott.) *2*, *S. emarginatum*. (After Seward.) From Lotsy.

Order 2. Sphenophyllales (132)

This small iosporous group of plants is only known in the fossil condition from palaeozoic rocks. It is characterised by the wedge-shaped, undivided, or dichotomously branched leaves being borne in whorls, usually of six members (Fig. 504).

The species of *Sphenophyllum* which lived from the Devonian to the Permian periods were herbaceous land-plants with elongated internodes, and were apparently scrambling climbers. The stems, which underwent secondary growth in thickness, had an axile stele without pith. The spike-like cones resembled somewhat those of *Equisctum*; each sporophyll bore one to four homosporous sporangia (Fig. 504). Sometimes as in *Cheirostrobus* the sporophylls were more complicated.

As characters common to the Equisetinae may be mentioned the smallness of the leaves relatively to the stem, and, in contrast to other Pteridophyta, their arrangement in whorls; the stem is segmented into nodes and internodes. The sporophylls are always different from the assimilating leaves; they have mostly the form of a centrally stalked, peltate expansion, from the lower side of which a number of sporangia hang, and they are associated in terminal spike-like cones. The prothalli are green and develop outside the spores.

The two Orders have the following distinguishing characters:

1. *Equisetales:* Leaves scale-like or small. Existing forms isosporous herbs without secondary growth in thickness; heterosporous dendroid forms with secondary thickening are known as fossils.

2. *Sphenophyllales:* Leaves with wedge-shaped lamina; isosporous (perhaps occasionally heterosporous) herbs with secondary thickening; only known as fossils.

The Equisetinae had their maximum development in palaeozoic times and, with the exception of a single genus, are extinct.

CLASS V.

Isoëtinae (137)

The only family is that of the **Isoëtaceae** with a single genus *Isoëtes*. The species of *Isoëtes* are perennial plants, growing either on damp soil or submerged in water. The stem is short and tuberous, rarely dichotomously branched, bearing below a tuft of dichotomously-branching roots, and above a thick rosette of long, stiff, awl-shaped leaves. The stem is characterised by a secondary growth in thickness by means of a cambium; this produces to the outer side cortex (without phloem) and to the inner side secondary phloem and xylem. The leaves are traversed longitudinally by four air-passages, and expand at the base into a broad sheath. On the inner side of the fertile leaves, above their point of insertion, is an elongated pit, the FOVEA, containing a large sessile sporangium. A LIGULE, in the form of a triangular membrane, is inserted above the fovea (Fig. 505), and serves to secrete mucilage.

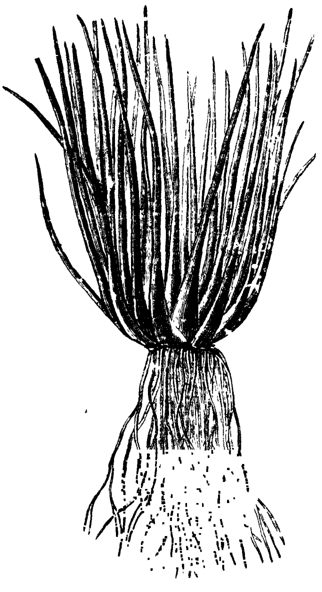


FIG. 505.—*Isoëtes lacustris.* (¼ nat. size.)

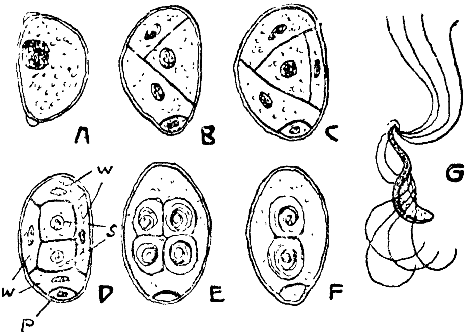


FIG. 506.—*A-F*, *Isoëtes setacea* (× 640). *A*, Microspore seen from the side. *B-D*, Segmentation of the spore; *p*, prothallial cell; *w*, the four cells of the wall *s*, spermatogenous cells. *E*, The four spermatozoid mother-cells are surrounded by the disorganised cells of the wall; surface view. *F*, The same in side view. *G*, *Isoetes Malinverniana*, spermatozoid (× 780). (After BELAJEFF.)

The MACROSPORANGIA are situated on the outer leaves of the rosette; the MICROSPORANGIA on the inner. Both are traversed by plates of tissue or trabeculae, and are in this way imperfectly divided into a series of chambers. Numerous macrospores are formed in the macrosporangium. The spores are set free by the decay of the sporangial walls.

The dioecious PROTHALLI are greatly reduced. The male prothallium (Fig. 506) arises within the spore, by the formation of a small, lenticular, vegetative cell (*p*), and a larger cell, the rudiment of a single antheridium. The larger cell divides further into four sterile peripheral cells (*w*), which completely enclose two central spermatogenous cells. From each of the latter arise, in turn, two spermatozoid mother-cells, four in all, each of which, when liberated by the rupture of the spore-wall, gives rise to a single, spirally-coiled, multicilate spermatozoid.

The female prothallium (Fig. 507), also remains enclosed within the macrospore, and is incapable of independent growth. The nucleus first divides into numerous, parietal daughter-nuclei before the gradual formation of the cell-walls, which takes place from the apex of the spore to the base. As a result of this process the whole spore becomes filled with a prothallium, at the apex of which the archegonia are developed. The development of the embryo takes place without the differentiation of apical cells.

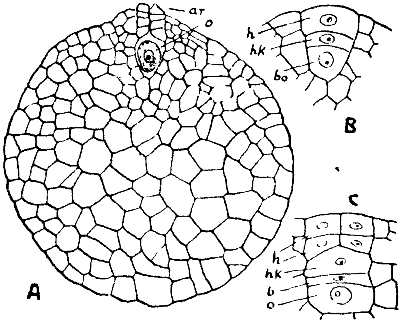


FIG. 507.—*Isoetes echinospora.* *A*, Female prothallium; *ar*, archegonium; *o*, egg-cell. *B*, *C*, Development of the archegonium from a superficial cell; *h*, neck-cells; *hk*, neck-canal-cell; *b*, ventral canal-cell; *o*, egg-cell. (× 250. After CAMPBELL.)

The Isoëtinae are characterised by their peculiar habit, and by their leaves being large in comparison with the stem. The heterospory and the extreme reduction of the sexual generation indicate a highly evolved group; the existing forms are to be regarded as the remains of a class of plants which contained numerous forms in earlier geological periods (Cretaceous). On account of the possession of a ligule they are frequently placed in relationship with the Selaginellales and Lepidodendrales; they differ fundamentally from these, however, by their multiciliate spermatozoids and the absence of a suspensor in the embryo.

CLASS VI

Filicinae (Ferns) (1, 93, 112, 115, 123)

All the Filicinae have large leaves on the lower side of which numerous sporangia are borne. They include three Sub-Classes:

1. **Eusporangiatae.**
2. **Leptosporangiatae.**
3. **Hydropterideae.**

The name Eusporangiatae comes from the fact that the sporangia have firm walls composed of several layers of cells, while the sporangial wall consists of only a single layer of cells in the Leptosporangiatae. In the Eusporangiatae the sporangium develops from several cells, in the Leptosporangiatae from one epidermal cell. In the Hydropterideae the sporangial wall is a single layer of cells.

Sub-Class I. Eusporangiatae

Order 1. Ophioglossales (117)

European examples of this order, the single Family of which (Ophioglossaceae) which contains only a few species, are afforded by *Ophioglossum vulgatum*, Adder's

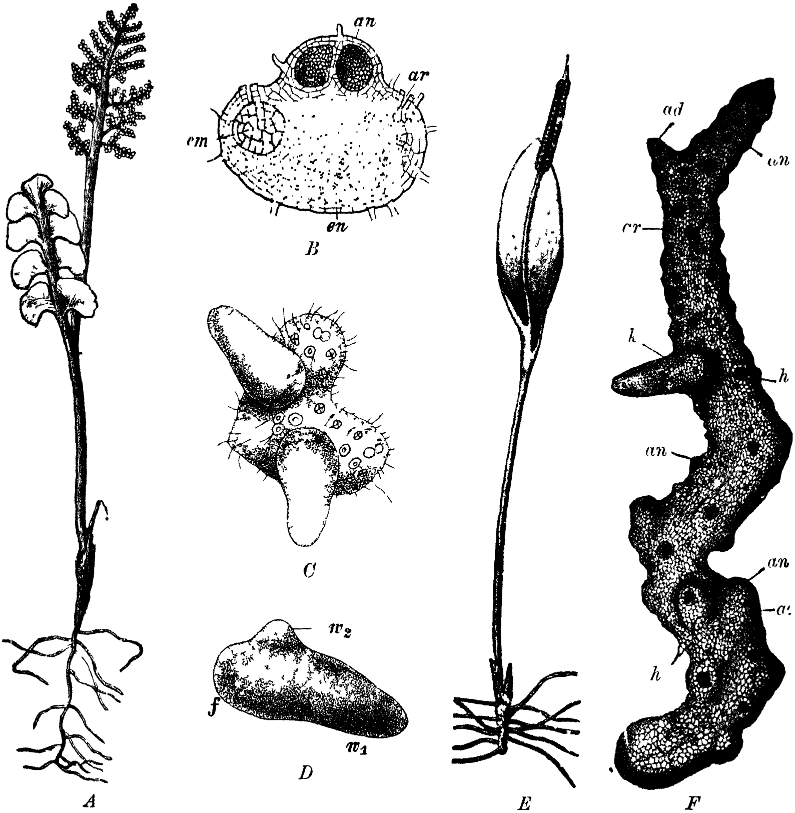


Fig. 508.—A, *Botrychium lunaria*. Sporophyte (½ nat. size) *B*, Transverse section of the prothallus; *an*, antheridium; *ar*, archegonium; *em*, embryo; *en*, fungal hyphae (× 45). *C*, Prothallus bearing two embryos, the roots of which have emerged (× 16). *D*, Embryo with the first and second roots (w_1, w_2) and foot (*f*) (× 16) *E*, *Ophioglossum vulgatum* Sporophyte showing the bud for the succeeding year. (½ nat size) *F*, *Ophioglossum vulgatum*. Prothallus. *an*, antheridia; *ar*, archegonia; *k*, young plant with the first root; *ad*, adventitious branch; *h*, fungal hyphae. (× 15 *B-D*, *F* after Bruchmann)

Tongue (Fig. 508 *E*), and *Botrychium*, Moonwort (Fig. 508 *A*). Both have a short stem, from which only a single leaf unfolds each year. The leaves in both cases are provided with leaf-sheaths. In *Ophioglossum* the leaf is tongue-shaped, in *Botrychium* it is pinnate. These leaves bear on their upper side a fertile segment arising near the upper end of the leaf-stalk. This fertile segment in *Ophioglossum* is simple and cylindrical, with the sporangia sunk in two rows ; in *Botrychium* it is pinnately branched in the upper part, and thickly beset on the upper side with large, nearly spherical sporangia. The course of the vascular bundles and occasional reversions indicate that the fertile segment is derived from the union of two basal pinnae.

The Ophioglossaceae are isosporous. Our knowledge of the peculiar monoecious PROTHALLI of the Ophioglossaceae is largely due to BRUCHMANN ; they are long-lived, subterranean, saprophytic, tuberous bodies without chlorophyll but inhabited by a mycorrhizal fungus. In *Ophioglossum* (Fig. 508 *F*) they are cylindrical and radially symmetrical, simple or branched ; in *Botrychium* (Fig. 508 *B*, *C*) they are oval or heart-shaped and dorsiventral. The antheridia (Fig. 509) and archegonia (Fig. 510) are sunk in the tissue of the prothallus. The antheridium encloses a large spherical mass of spermatozoid mother-cells which are set free when mature by the separation of a cover-cell due to the mucilaginous change in its wall. The spermatozoids have a spirally wound body and numerous cilia; a small vesicle is adherent to the spermatozoid (Fig. 509 *E*). The antheridia originate from single superficial cells (Fig. 509 *A*-*C*), as do also the archegonia (Fig. 510 *A*-*C*). The slightly projecting neck of the latter opens after the neck-canal-cell has swollen and disintegrated ; the oosphere (*o*) remains in the sunken venter. In some species the embryo leads a subterranean existence for several years. The primary root is first formed and soon projects from the archegonium (Fig. 508 *C*, *F*, *k*) ; later the first leaf and the apical cell of the stem are differentiated. In some species of *Botrychium* the embryo forms an elongated multicellular suspensor at the end of which the proper embryonic mass is formed. In this an agreement with the Lycopodinae is evident (cf. Fig. 490 and Fig. 495), which do not in other respects show any close relationship to the Eusporangiatae.

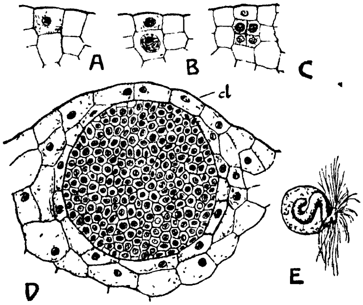


FIG. 509.—*Ophioglossum vulgatum*. *A*-*C*, Stages in the development of the antheridium from a superficial cell ; the upper cell in *C* gives rise to the cover-cells, the lower to the mother-cells of the spermatozoids. *D*, Antheridium not yet opened ; *d*, cover-cells. *E*, Spermatozoid. (After BRUCHMANN.)

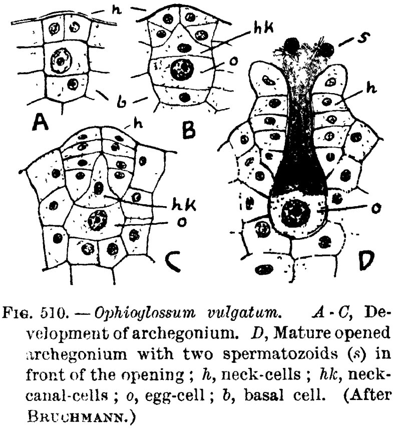


FIG. 510. — *Ophioglossum vulgatum*. *A*-*C*, Development of archegonium. *D*, Mature opened archegonium with two spermatozoids (*s*) in front of the opening ; *h*, neck-cells ; *hk*, neck-canal-cells ; *o*, egg-cell ; *b*, basal cell. (After BRUCHMANN.)

Order 2. Marattiales.

The plants belonging to this Order are widely distributed in the tropics. They are isosporous, and have large fronds provided with a pair of stipules at the base. These are borne on the thickened tuberous stem. The prothalli, though they contain an endophytic fungus, grow on the surface of the soil as green heart-shaped structures. They are rather thick and long-lived and resemble some Liverworts in appearance. In some cases the embryo is borne on a suspensor. One of the best-known representatives is *Angiopteris,* which is frequently cultivated in hot-houses.

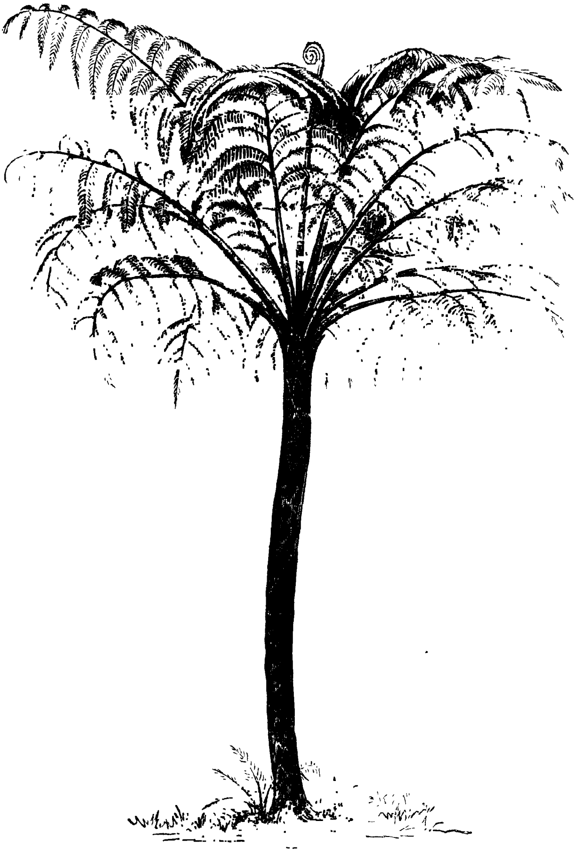


FIG. 511.—*Alsophila crinita.* A Tree-Fern growing in Ceylon. (Reduced.)

Sub-Class II. Leptosporangiatae (Filices)

The Leptosporangiatae comprise a large number of genera with numerous species, being widely distributed in all parts of the world. They attain their highest development in the tropics. The Tree-Ferns (*Cyathea, Alsophila, Dicksonia*), which include the largest representatives of the order, occur in tropical countries, and characterise the special family of the Cyatheaceae. The stem of a Tree-Fern (Fig. 511) is woody and unbranched: it bears at the apex a rosette of pinnately compound leaves or fronds, which are produced in succession from the terminal bud, and leave, when dead, large leaf-scars on the trunk. The stem is attached to the soil by means of numerous adventitious roots, and is also covered by a coating of roots. The majority of ferns, however, are herbaceous, and possess a creeping or erect rhizome, terminating usually in a rosette of pinnate or deeply-divided leaves. Such a habit and growth are illustrated by the common Male Fern *Dryopteris* (*Aspidium*) *filix mas*, the rhizome of which is official (Fig. 512). The leaves of *Polypodium vulgare* are pinnate, and spring singly from the upper side of the creeping branched rhizome. In other cases the leaves may be simple and undivided, as in the Hart's-Tongue Fern, *Scolopendrium vulgare* (Fig. 513). In the tropics many herbaceous Ferns grow as epiphytes on forest trees.

When young, the leaves are coiled at the tips (Fig. 511), a peculiarity common to the Ferns as a whole. Unlike the leaves of most Phanerogams, those of the Ferns continue to grow at the apex until their full size is attained.

The venation or course of the vascular bundles in the lamina, provides important characters for the systematic grouping of the Leptosporangiatae. While only a single median bundle is present in the simple leaves of the Horsetails and Club Mosses, the veins in the fern leaf are branched in various ways. They may be dichotomous or pinnate with free endings, or may anastomose to form a network. The ultimate branches may end blindly in the meshes of this.

Peculiar brownish scales (paleae, ramenta), often fringed and consisting of a single layer of cells, invest the stems, petioles, and sometimes also the leaves of most Ferns.

The sporangia are generally produced in large numbers, on the under side of the leaves. The sporophylls, as a rule, resemble the sterile foliage-leaves. In a few genera a pronounced heterophylly is exhibited: thus in the Ostrich Fern, *Struthiopteris germanica*, the dark brown sporophylls are smaller and less profusely branched, standing in groups in the centre of a rosette of large foliage-leaves. *Blechnum spicant* is another example.

In the different Families, differences in the form, position, and structure of the SPORANGIA are manifested.

The sporangia of the **Polypodiaceae**, in which family the most familiar and largest number of species are comprised, are united in groups or SORI on the under side of the leaves. They are borne on a cushion-like projection of tissue termed the RECEPTACLE (Fig. 512 *A*), and in many species are covered by a protective membrane, the INDUSIUM, which is an outgrowth of the tissue of the leaf (Fig. 512 *B*, *C*). Each sporangium arises by the division of a single epidermal cell (Fig. 486), and consists, when ripe (Fig. 514), of a capsule attached to the receptacle by a slender multicellular stalk, containing a large number of spores, which only in a few genera (*Asplenium*, *Aspidium*, *Acrostichum*, etc.) are surrounded by a perispore. The wall of the

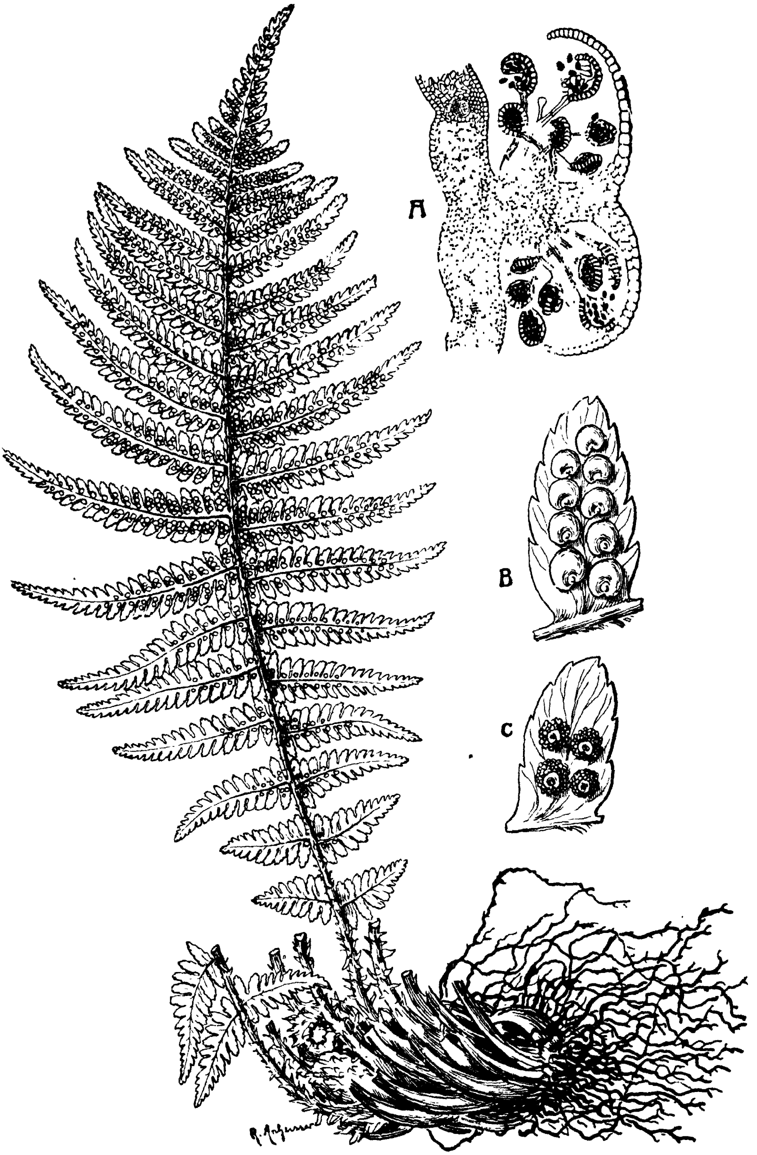


FIG. 512.—*Dryopteris* (*Aspidium*) *filix mas* ($\frac{1}{6}$ nat. size). *A*, Sorus in vertical section. (× 20. After KNY.) *B*, Pinna with young sori still covered by the indusia. *C*, Somewhat older sori with withered indusia. (Slightly magnified.) *OFFICIAL*.

capsule is formed of a single layer of cells. A row of cells with strongly thickened radial and inner walls, extending from the stalk over the dorsal side and top to the middle of the ventral side of the capsule, are specially developed as a ring or ANNULUS, by means of which the dehiscence of the sporangium is effected. This type of annulus is characteristic of the Polypodiaceae.

On drying of the wall of the sporangium the cohesion of the remaining water in the cells of the annulus draws in the thin outer walls of these cells; this causes the annulus to shorten and determines the dehiscence of the sporangium by a tranverse slit between the broad, unthickened terminal cells of the annulus. When the diminishing water-drop ruptures and the pull exerted by the cohesive power of the water suddenly gives way, the annulus returns by its own elasticity to its original position, thus effecting the dispersal of the spores. The sporangium remains open owing to the drying and contraction of the thin cell-walls (cf. Fig. 189) (^{118}).

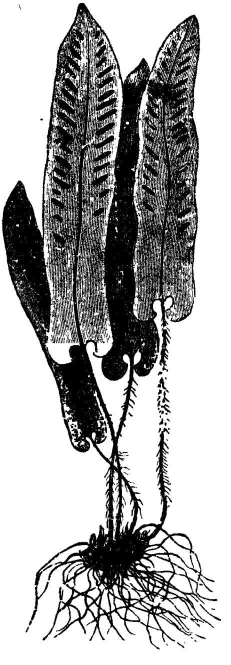


FIG. 513.—*Scolopendrium vulgare.* (¼ nat. size.)

The form and insertion of the sori, the shape of the indusium when present, or its absence, all constitute important criteria for distinguishing the different genera. The sori of *Scolopendrium* (Fig. 513) are linear, and covered with a lip-shaped indusium consisting of one cell-layer. They are so disposed in pairs that they appear to have a double indusium opening in the middle. In the genus *Dryopteris* (*Aspidium*) (Fig. 512), on the other hand, each sorus is orbicular in form and covered by a peltate or reniform indusium attached to the apex of the placenta; a glandular hair is frequently present on the stalk of the sporangium (Fig. 514 *A*). The sori of *Polypodium vulgare* are also orbicular, but they have no indusia. In the common Bracken, *Pteridium aquilinum*, the sporangia form a continuous line along the entire margin of the leaf, which folds over and covers them.

Besides the Polypodiaceae the Ferns include other families, mainly represented in the tropics, the sporangia of which differ in the construction of the annulus and in the mechanism of their dehiscence. The sporangia of the **Cyatheaceae,** to which family belong principally the Tree-Ferns, are characterised by a complete annulus extending obliquely over the apex of the capsule (Fig. 514 *B*, *C*). The **Hymenophyllaceae**, often growing as epiphytes on Tree-Ferns, have also sporangia, with a complete, oblique annulus. They have leaves with a delicate membranous lamina, and while mainly tropical are represented in Britain (*H. tunbridgense*). The sporangia of the **Schizaeaceae** and **Gleicheniaceae,** on the other hand, have a transversely-placed annulus which, in the former (Fig. 514 *D*), is close to the tip and in the latter above the middle of the sporangium, while in the **Osmundaceae,** of which the Royal Fern, *Osmunda regalis*, is a familiar example, the annulus is represented merely by a group of thick-walled cells just below the apex of the sporangium (Fig. 514 *E*). In the three last-named families the sporangia open by a median split; in the three preceding families the dehiscence is transverse or oblique. There are thus two main groups of longicidal and brevicidal Leptosporangiatae, the Eusporangiatae coming closer to the former (119).

All the members of the Filices are isosporous. The PROTHALLIUM has usually the form of a small, flat, heart-shaped thallus (Fig. 482), bearing the antheridia and archegonia on the under side, which is turned from the light.

In certain Hymenophyllaceae (*Trichomanes*) the prothallium is filamentous and branched, resembling in structure the protonema of the Mosses, and producing the antheridia and archegonia on special multicellular lateral branches (Fig. 515).

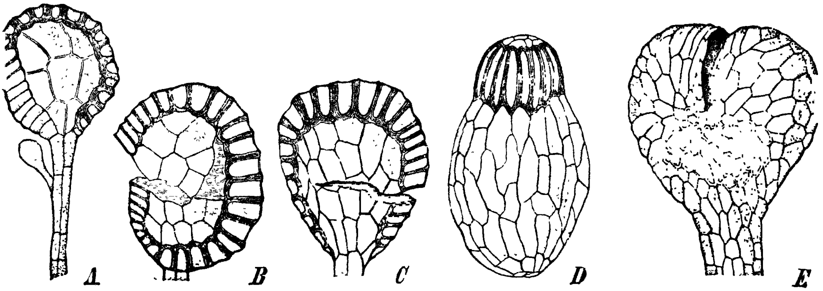


FIG. 514.—Sporangia. *A*, *Dryopteris* (*Aspidium*) *filix mas*; there is a glandular hair at the base. *B* and *C*, *Alsophila armata*, seen from the two sides. *D*, *Anemia caudata*. *E*, *Osmunda regalis*. (*A*-*D* × 70 orig.; *E* × 40. After LURSSEN.)

The ANTHERIDIA and ARCHEGONIA (120) are similarly constructed in nearly all Leptosporangiatae, and present differences from those of the Eusporangiate Ferns. The antheridia are spherical projecting bodies (Fig. 516), arising on young prothallia by the septation and further division of papilla-like protrusions from single superficial cells. When mature, each antheridium consists of a central cavity, filled with spermatozoid mother-cells, and enclosed by a wall formed of two ring-shaped cells and a cap-cell; in some families the cap-cell is divided into two or more cells, but usually remains undivided in the Polypodiaceae. The spermatogenous cells are produced by the division of the central cell. They are discharged from the antheridium by the pressure exerted by the swollen ring-cells, and the consequent rupturing of the cell. Each rounded mother-cell thus ejected liberates a spirally coiled spermatozoid. The anterior extremity of the spermatozoid is beset with numerous cilia, while attached to its posterior end is a small vesicle which contains a number of granules, and represents the unused remnant of the contents of the mother-cell.

The archegonia (Fig. 517) arise from the many-layered median portion of older prothallia. They are developed from single superficial cells, and consist of a ventral portion, embedded in the prothallium, and a neck portion. The neck, which is longer than in the case of the Eusporangiatae, consists of a wall composed of a single layer of cells made up of four cell-rows; it encloses the elongated neck-canal-cell. The ventral portion contains the large egg-cell and the ventral-canal-cell immediately above it. As the archegonium matures, the canal-cells become disorganised, and fill the canal with a strongly refractive mucilaginous substance. This swells on the admission of water, and, rupturing the neck at the apex, is discharged from the archegonium, which is now ready for fertilisation. The development of the embryo is represented in Fig. 483.

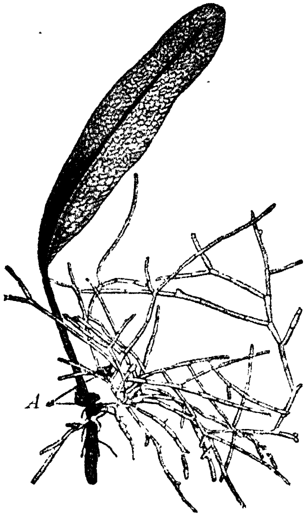


Fig. 515.—*Trichomanes rigidum.* Portion of a prothallus with an archegoniophore (*A*) to which a young plant is attached. (After Goebel.)

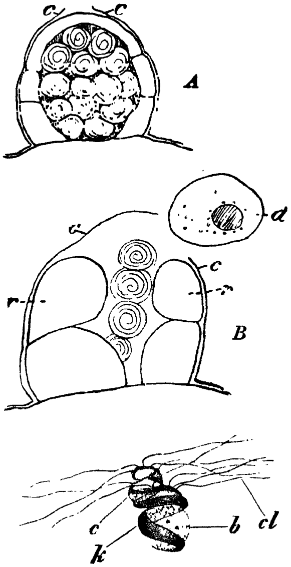


Fig. 516.—*A*, Mature antheridium of *Woodsia ilvensis*; the cuticle (*c*) is ruptured. *B*, Open antheridium; *d*, cap-cell; *r*, swollen annular cells. (After Schlumberger.) *C*, Spermatozoid of *Struthiopteris germanica*; *k*, nucleus; *cl*, cilia; *b*, vesicle derived from the vacuole; *c*, cytoplasm. (× 850. After Shaw.)

In certain ferns the sporophyte may originate on the prothallus by a process of budding or direct vegetative growth; the sexual organs are not formed or they take no part in the production of the plant (apogamy). Conversely the prothallus may arise directly, without the intervention of spores, from the tissues of the leaf (apospory) (cf. p. 590).

Official.—*Dryopteris* (*Aspidium*) *filix mas*, provides filix mas.

The long silky brown hairs from the base of the leaf-stalks of various Tree-Ferns, especially *Cibotium Barometz,* and other species, of this genus, in the East Indies and the Pacific Islands, are used as a styptic, and also for stuffing cushions, etc.

Sub-Class 3. Hydropterideae (Water-Ferns) (121-123)

The Water-Ferns include only a few genera, which are more or less aquatic in habit, growing either in water or marshy places. They are all heterosporous. The macro- and micro-sporangia are enclosed in special receptacles at the base of the leaves, constituting sporangial fructifications or sporocarps. The wall of the sporangium, which consists of a single layer of cells, has no annulus. The spores are surrounded by a specially developed perisporium.

The Water-Ferns are divided into two families: *Salviniaceae*, with two genera, and *Marsiliaceae*, including three genera.

The **Salviniaceae** contain only free-floating aquatic plants belonging to the two genera *Salvinia* and *Azolla*. In *Salvinia natans*, as representative of the first genus, the sparingly-branched stem gives rise to three leaves at each node. The two upper leaves of each whorl are oval in shape, and developed as floating foliage-leaves; the third, on the other hand, is submerged, and consists of a number of pendent, filamentous segments which are densely covered with hairs, and assume the functions of the missing roots. The sporocarps have an entirely different mode of development from those of the Marsiliaceae; they are spherical, and are borne in small groups on the submerged leaves at the base of the filamentous segments (Fig. 518 *A*). The sporangia are produced within the sporocarp from a column-like receptacle, which corresponds in origin to a modified leaf-segment. The envelope of the sporocarp is equivalent to an indusium; it arises as a new growth in the form of an annular wall, which is at first cup-shaped, but ultimately closes over the receptacle and its sorus of sporangia.

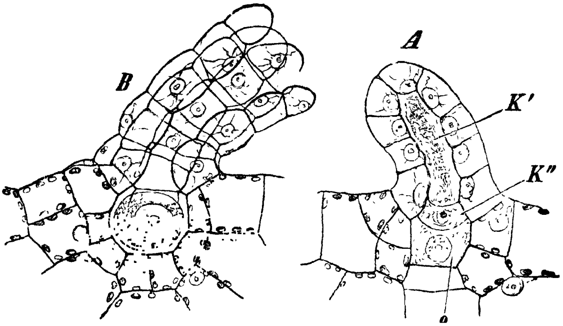


FIG. 517.—*Polypodium vulgare.* *A*, Young archegonium not yet open; *K'*, neck-canal-cell; *K"*, ventral-canal-cell; *o*, egg-cell; *B*, mature archegonium, open. (× 240. After STRASBURGER.)

The second genus, *Azolla*, is chiefly tropical, represented by small floating plants, profusely branched, and beset with two-ranked closely crowded leaves. Each leaf consists of two lobes, of which the upper floats on the surface of the water, while the lower is submerged, and assists in the absorption of water. The sporocarps are nearly spherical, and produced usually in pairs on the lower lobes of the leaves of some of the lateral branches. A small cavity enclosed within the upper lobe, with a narrow orifice opening outwards, is always inhabited by filaments of the Blue Green Alga, *Anabaena azollae*. From the fact that hairs grow out of the walls of the cavity between the algal filaments, the existence of a symbiotic relation between the two plants would seem to be indicated. *Azolla*, unlike *Salvinia*, possesses long slender roots developed from the under side of the stem.

To the **Marsiliaceae** belongs the genus *Marsilia*, of which the European *M quadrifolia* (Fig 519 *A*) may be taken as an example This species has a slender, creeping, branched axis, bearing at intervals single leaves Each leaf has a long

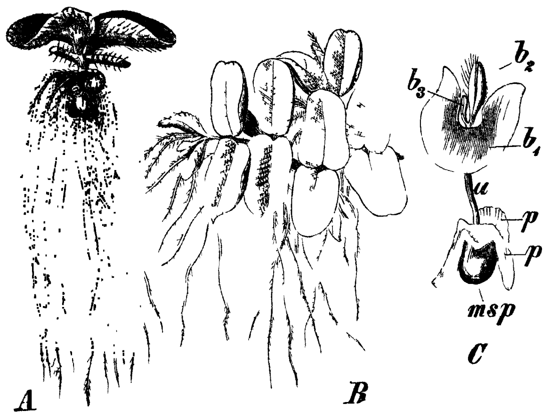


Fig 518 —*Salvinia natans* *A*, Seen from the side *B* from above (after Bischoff reduced) *C*, An embryonic plant *msp* macrospore *p* prothallium *a* stem b_1 b_2 b_3 the first three leaves b_1, the so called scutiform leaf (× 15 After Pringsheim.)

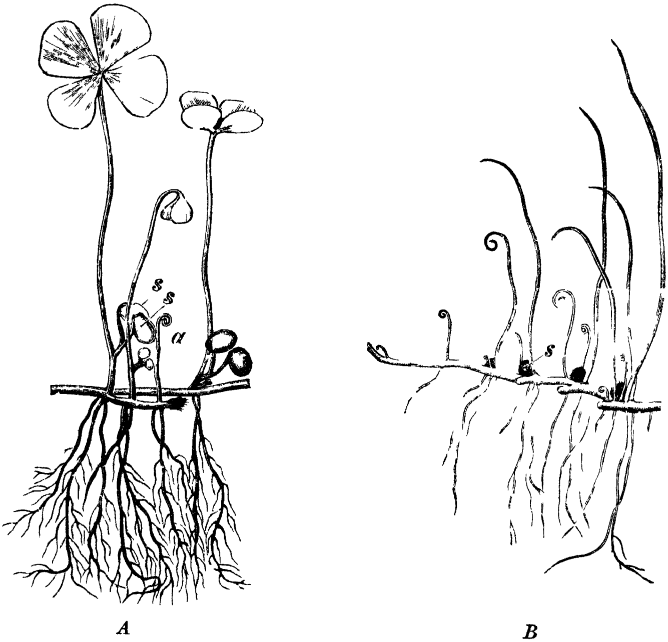


Fig 519 —*A*, *Marsilia quadrifolia* *a*, young leaf *s* sporocarps *B*, *Pilularia globulifera*, *s*, sporocarp (After Bischoff, reduced)

erect petiole, surmounted by a compound lamina composed of two pairs of leaflets inserted in close proximity. The stalked oval sporocarps (*s*) are formed in pairs above the base of the leaf-stalk; in other species they are more numerous. Each of them corresponds in development to the sterile lamina, but is not divided into pinnae.

Pilularia also grows in bogs and marshes. *P. globulifera* is found in Britain. It differs from *Marsilia* in its simple linear leaves, at the base of which occur the spherical sporocarps, which arise singly from the base of each sterile leaf-segment; the sporocarp corresponds to a segment of the leaf (Fig. 519 *B*). The young leaves, as in the Filices, are circinate in both genera.

In the structure of the sporangia and spores, and in the development of the prothallia, the Hydropterideae differ in some respects from the Filices. These differences may be best understood on reference to *Salvinia natans* (121) as an example. The sporocarps contain either numerous microsporangia or a smaller number of macrosporangia (Fig. 520 *A*, *ma*, *mi*). In development and structure both forms of sporangia resemble the sporangia of the Leptosporangiate Ferns; they are stalked, and have, when mature, a thin wall of one cell-layer, but no annulus (*B*, *D*). The MICROSPORANGIA enclose microspores, which, as a result of their development in tetrads from the mother-cells, are disposed in groups of four (*C*), and embedded in a hardened frothy mass filling the cavity of the sporangium. This frothy interstitial substance is derived from the single layer of tapetal cells.

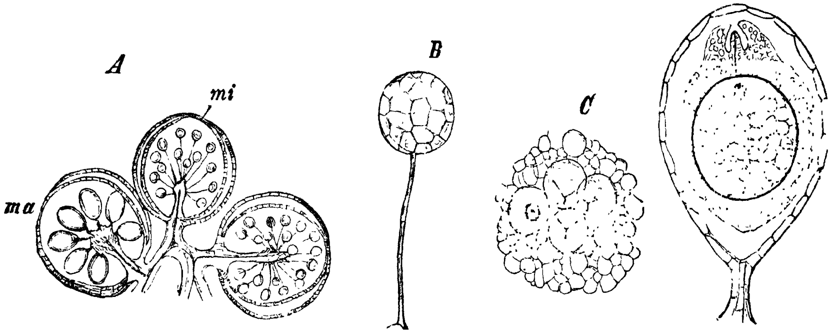


FIG. 520.—*Salvinia natans*. *A*, Three sporocarps in median longitudinal section; *ma*, macrosporocarp; *mi*, microsporocarp (× 8); *B*, a microsporangium (× 55); *C*, portion of the contents of a microsporangium, showing four microspores embedded in the frothy interstitial substance (× 250); *D*, a macrosporangium and macrospore in median longitudinal section (× 55). (After STRASBURGER.)

The microspores germinate within the microsporangium, which does not open; each germinating microspore puts out a short tubular male-prothallium, which pierces the sporangial wall. Two antheridia are developed in this by successive divisions (Fig. 521). Each antheridium produces four spermatozoids, which are set free by the rupture of the cell-walls. The male prothallium is thus greatly reduced.

The MACROSPORANGIA are larger than the microsporangia, but their walls consist similarly of one cell-layer (Fig. 520 *D*). Each macrosporangium produces only a single large macrospore, which develops at the expense of the rest of the thirty-two spores originally formed. The macrospore is densely filled with large angular protein-grains, oil-globules, and starch-grains; at its apex the protoplasm is denser and contains the nucleus; the membrane of the spore is covered by a dense brown exospore, which in turn is enclosed in a thick frothy envelope, the perispore, investing the whole spore and corresponding to the interstitial substance of the microspores, and like this formed from the dissolution of the tapetal cells. The macrospore remains within the sporangium, which is eventually set free from the mother-plant and floats on the surface of the water. On the germination of the macrospore, a small-celled female prothallium is formed by the division of the denser protoplasm at the apex, while the large underlying cell does not take part in the division, but from its reserve-material provides the developing prothallium with nourishment. The spore-wall splits into three valves, the sporangial wall is ruptured, and the green prothallium protrudes as a small saddle-shaped body. On it three to five archegonia are produced, but only the fertilised egg-cell of one of them develops into an embryo, the foot of which remains for a time sunk in the venter of the archegonium (Fig. 522). The first leaf of the germ-plant is shield-shaped (Fig. 518 *C*) and floats on the surface of the water.

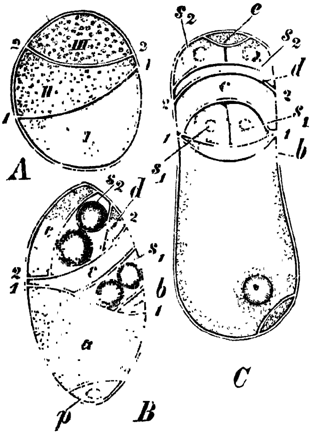


FIG. 521.—*Salvinia natans.* Development of the male prothallium. *A*, Division of the microspore into three cells *I-III* (× 860); *B*, lateral view; *C*, ventral view of mature prothallium (× 640). Cell *I* has divided into the prothallium cells *a* and *p*; the latter is the rhizoid cell; cell *II* into the sterile cells *b*, *c*, and the two cells s_1, each of which has formed two spermatozoid mother-cells; cell *III* into the sterile cells *d*, *e*, and the two cells s_2. The cells s_1s_1 and s_2s_2 represent two antheridia; the cells *b*, *c*, *d*, *e*, their wall-cells. (After BELAJEFF.)

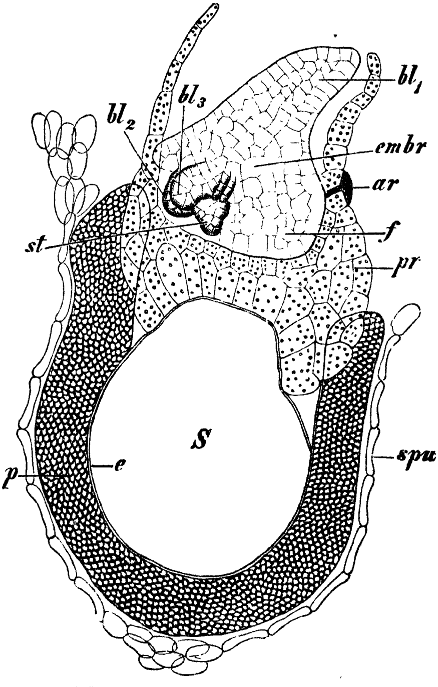


FIG. 522.—*Salvinia natans.* Embryo in longitudinal section; *pr*, prothallium; *S*, spore-cell; *e*, exospore; *p*, perispore; *spw*, sporangial wall; *ar*, archegonium; *embr*, embryo; *f*, foot; bl_1, bl_2, bl_3, the first three leaves; *st*, apex of stem. (× 100. After PRINGSHEIM.)

The development of *Azolla* (121a) proceeds in a similar manner, but the sporangia and spores exhibit a number of distinctive peculiarities. The micro- and macrosporocarps at first develop alike; in each a single macrosporangium is laid down surrounded by the tubular indusium, and from the stalk of the macrosporangium the microsporangia grow out. In the microsporocarp only the microsporangia develop; in the macrosporocarp, on the other hand, only the macrosporangium becomes mature. The sixty-four spores of the microsporangia are aggregated into several nearly spherical balls or massulae, formed from the interstitial substance derived from the protoplasm of the tapetal cells. Each massula, enclosing a number of spores, is beset externally with barbed, hook-like outgrowths of the interstitial substance (glochidia).

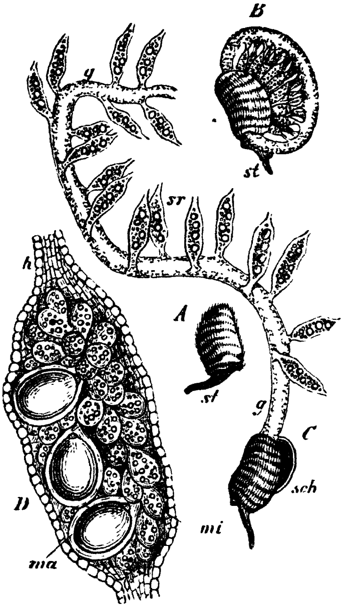


FIG. 523. —*Marsilia salvatrix.* *A*, Sporocarp (nat. size); *st*, stlak. *B*, Sporocarp opening in water, showing the emerging mucilaginous cord. *C*, The mucilaginous cord (*g*) ruptured and fully extended; *sr*, soral chambers; *sch*, hard shell of the sporocarp. *D*, An immature sorus; *ma*, macrosporangia; *mi*, microsporangia. (After J. SACHS and J. HANSTEIN.)

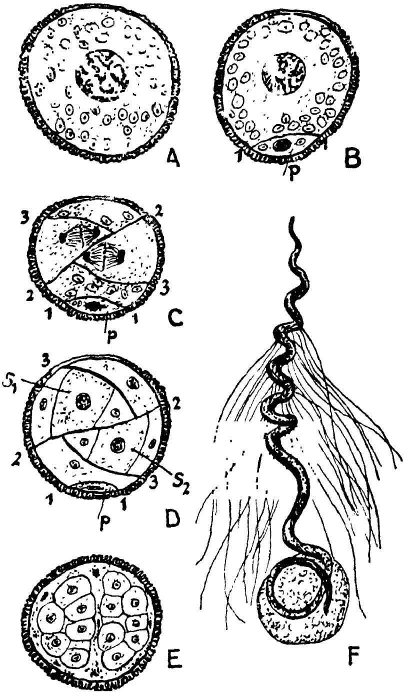


FIG. 524.—*Marsilia quadrifolia.* Development of the male prothallus from the spore. *A*, The spore; *B*, a small prothallial cell (*p*) is cut off by the wall (*1*); *C* and *D*, further divisions, s_1, s_2, the mother-cells of the spermatogenous tissue in the two antheridia; *E*, mature condition, two groups of sixteen spermatozoids having developed from s_1 and s_2, lie in the substance derived from the breaking down of the peripheral sterile cells *F*, a spermatozoid, highly magnified. (After LESTER W. SHARP.)

On the rupture of the sporangia the massulae are set free in the water, and are carried to the macrospores, to which they become attached. In the macrosporangium thirty-two macrospores are laid down, but only one comes to maturity; in the course of its development it supplants all the other sporogenous cells, and finally the sporangial wall itself becomes flattened against the inner wall of the sporocarp, frequently undergoing at the same time partial dissolution. The macrospore is enveloped by a spongy perispore, whose outer surface exhibits numerous depressions and protuberances prolonged into filaments. At the apex of the spore the perispore expands into three pear-shaped appendages. The massulae become attached to the perispore. The wall of the sporocarp is ruptured at its lower portion, the apical portion remaining attached to the spore in the form of an ampulla-like covering. The formation of the prothallia is effected in essentially the same way as in *Salvinia*, except that only one antheridium with eight spermatozoids arises on each of the small male prothallia protruding from a massula.

The sporocarps of the Marsiliaceae ([122]) have a more complicated structure: those of *Pilularia globulifera* are divided into four chambers, each with a single sorus; in the sporocarp of *Marsilia* there are numerous sori (14-18) disposed in two rows. The sori in both genera contain both micro- and macro-sporangia. These arise as in many ferns from superficial marginal cells and come to lie in cavities by the upgrowth of the surrounding tissue. The outer layers of this become differentiated to form a hard coat.

After a period of rest the sporocarps germinate in water. In *Pilularia* the tissue surrounding the sori swells, bursts the hard coat, and emerges as a mucilaginous mass; this contains the sporangia, from which, by further swelling of the walls, the spores become free. The development of the prothalli and fertilisation take place in the mucilaginous mass that persists for some days. The sporocarp of *Marsilia*, on the other hand, opens as two valves. A cartilaginous cord of tissue lying within the dorsal and ventral sutures of the sporocarp swells greatly, and splitting the ventral suture, emerges, bearing with it the sori, enclosed by membranous investments (Fig. 523).

From the microspore a reduced male prothallus is developed within the spore-membrane. This when mature contains two antheridia, each with sixteen spermatogenous cells, and liberates these as cork-screw-like, spirally-wound, motile spermatozoids bearing numerous cilia (Fig. 524).

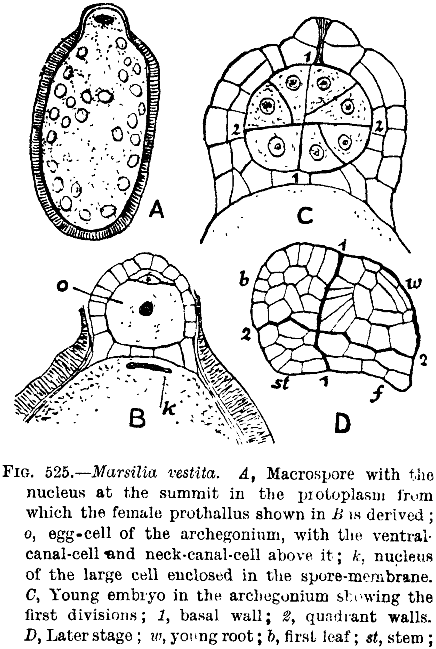


FIG. 525.—*Marsilia vestita*. *A*, Macrospore with the nucleus at the summit in the protoplasm from which the female prothallus shown in *B* is derived; *o*, egg-cell of the archegonium, with the ventral-canal-cell and neck-canal-cell above it; *k*, nucleus of the large cell enclosed in the spore-membrane. *C*, Young embryo in the archegonium showing the first divisions; *1*, basal wall; *2*, quadrant walls. *D*, Later stage; *w*, young root; *b*, first leaf; *st*, stem; *f*, foot. (*A* × 60; *B* × 360; *C* × 525; *D* × 260. After D. CAMPBELL.)

The thick-walled macrospore has, as in the case of *Salvinia*, denser protoplasm at the summit. This is cut off from the large cell enclosed in the spore-coat by a wall, and develops into a small green saddle-shaped prothallus composed of a few cells. This only forms a single archegonium and is thus greatly reduced (Fig. 525).

The embryogeny follows the type of the Leptosporangiate Ferns, the egg-cell dividing first by a longitudinally-placed basal wall and then by transverse walls into quadrants; these then divide to give the octants. The first leaf and the root arise from the two upper pairs of octants; the lower pairs give rise to the foot and the stem-apex (Fig. 525 *C*, *D*).

The prothallus grows for a time enclosing the embryo, and forms a few rhizoids from its lower cells. If fertilisation does not take place, a somewhat longer-lived prothallus results, which does not, however, form further archegonia.

A survey of the Filicinae shows that they all have RELATIVELY LARGE LEAVES which may be highly branched or be simple. The sporophylls may be similarly formed to the vegetative leaves or may differ more or less from them. They bear the sporangia usually ON THE LOWER SURFACE. The sporangia may be isolated or numbers may be grouped together in sori; in some cases they are enclosed by special segments of the leaf.

The three Sub-Classes may be briefly characterised thus: 1. *Eusporangiatae.* Mature sporangia with a firm wall composed of a number of layers of cells. Isosporous. Prothalli subterranean and colourless, or superficial and green, always with an endophytic fungus. Herbaceous. Leaf-base with stipules. The Eusporangiatae may be regarded as the most primitive of the three sub-classes on account of the slight differentiation of their shoot, and the less marked dorsiventrality of their prothallus.

2. *Leptosporangiatae.* Sporangia with a wall composed of one layer of cells and a special opening mechanism (annulus). Isosporous. Prothalli green, autotrophic, monoecious or dioecious. Plants herbaceous or dendroid, without secondary growth in thickness. Leaves variously shaped, circinately coiled when young, without stipules.

3. *Hydropterideae.* Sporangia with wall of one layer of cells; without annulus. Sori enclosed in sporocarps. Heterosporous. Prothalli always very much reduced, and developing within the spore. Aquatic or marsh-plants with creeping rhizomes.

The Eusporangiatae and Leptosporangiatae were already well developed in the Carboniferous period, the former coming somewhat earlier than the latter; the Hydropterideae make their first appearance in the Trias. While the Leptosporangiatae still exist in great numbers and variety (the Family Polypodiaceae alone contains several thousand species), the Eusporangiatae were more richly represented in earlier geological periods; they now consist of only two families containing few genera.

CLASS VII

Pteridospermae (Seed-Ferns) ($^{132, 134}$)

The Pteridospermae, which are also spoken of as Cycadofilicinae, are fossil plants which are known from the Lower Carboniferous. Their fronds were highly pinnate (*Sphenopteris*, Fig. 526), and the plant as a whole had the general habit of a tree-fern. The stem was unbranched or produced a few axillary branches (*Lyginodendron*). It had secondary growth in thickness by means of a cambium. This produced to the inside the radially seriated elements of the secondary wood around the large central pith; to the outside a zone of bast was formed (Fig. 527). The leaf-trace bundles can be followed inwards from the cortex through the secondary wood to join the strands of primary wood at the periphery of the pith. The roots also had secondary thickening.

The Pteridosperms were heterosporous. Their sporangia were borne on fronds that are scarcely to be distinguished from the fronds of the true Ferns. The eusporangiate microsporangia were situated on the lower side of certain pinnules or on modified portions of the leaf.

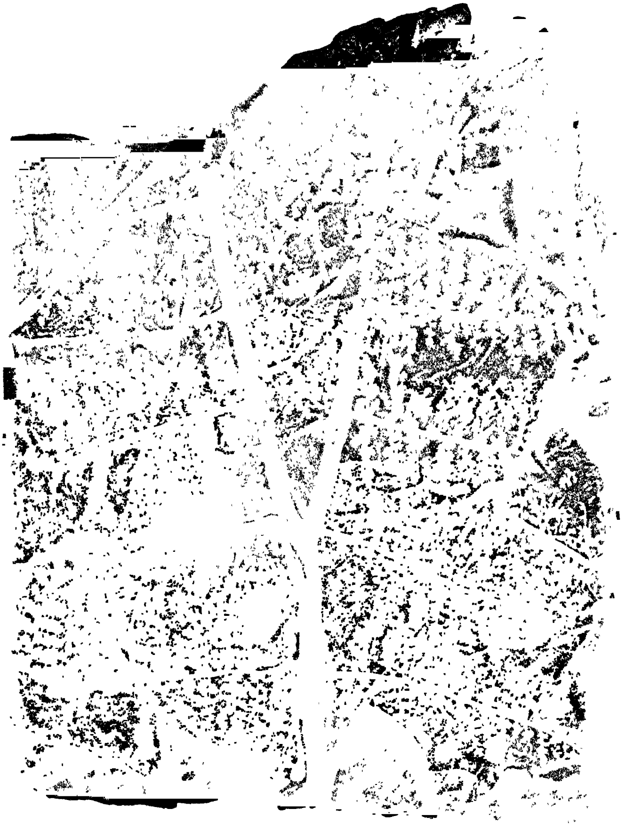


FIG. 526.—*Lyginodendron*. Frond. (*Sphenopteris Hoeninghausii*.) (Reduced ⅓. After POTONIÉ.)

The MACROSPORANGIUM, which had a firm wall, contained only one MACROSPORE, and this was coherent with the tissue of the macrosporangium. The latter was (as in the Lepidodendrales) surrounded by an INTEGUMENT open at the apex only. Around the whole structure there was frequently a cup-shaped upgrowth, the cupule (Figs. 528, 529). Into the opening of the integument (micropyle) there projected from below an outgrowth of the macrosporangium. This was hollow and formed a chamber around a conical central column. Since similar structures are met with among Gymnosperms (see p. 574), it may be assumed that the chamber in the Pteridosperms also served to receive the microspores, probably distributed by the wind. In this microspore-chamber the microspores would then liberate their spermatozoids. The embryo is still unknown.

The Pteridospermae possess the highest grade of organisation among the Pteridophytes. It is noteworthy that this stage had been already reached in the Carboniferous period. The group became extinct in the Permian.

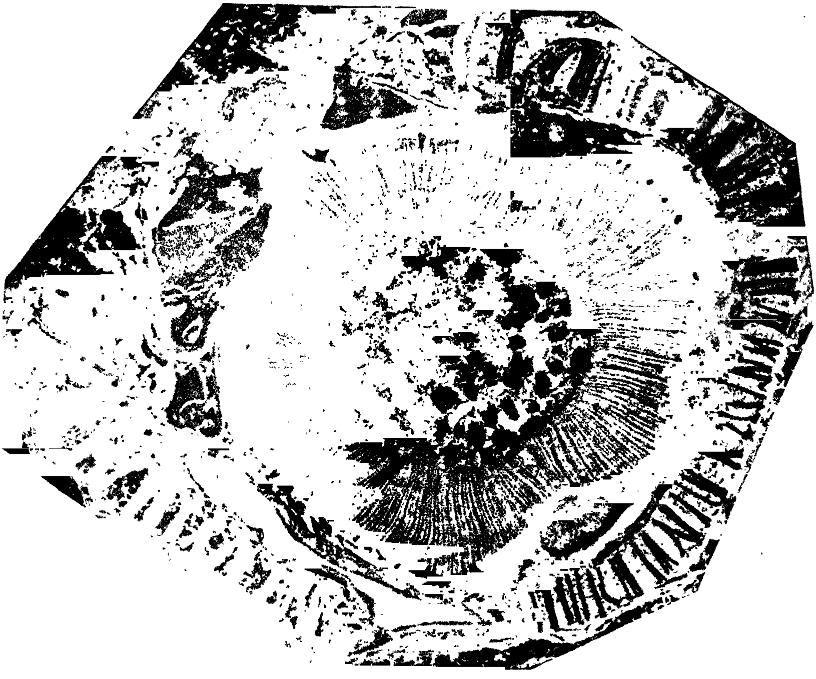


FIG. 527.—*Lyginodendron oldhamium.* Transverse section of stem. (× 2½. After SCOTT.)

Survey of the Pteridophyta

The Pteridophyta are plants the life-history of which is based on a regular ALTERNATION OF GENERATIONS (Fig. 530). The DIPLOID ASEXUAL GENERATION exhibits great variety, and is the larger and much the more highly differentiated stage in the life-history. Tracheides make their appearance as an entirely new feature in the sporophyte, and so facilitate the conduction of water in the plant that this can assume the form of a highly segmented and sometimes dendroid land-plant. This contrasts with the condition in the Bryophyta, which, for want of well-developed conducting tracts, are unable to attain any considerable size (89).

The ASEXUAL SPORES, the formation of which is associated with the reduction-division, are produced in sporangia. These are borne on sporophylls which are frequently more or less different in habit from the other leaves and are often associated in special cones (flowers). In the lower forms the spores are all of one kind (ISOSPORY), but in higher forms a differentiation into microspores and macrospores takes place (HETEROSPORY). In the latter case the prothalli are also distinguished into smaller male and larger female prothalli.

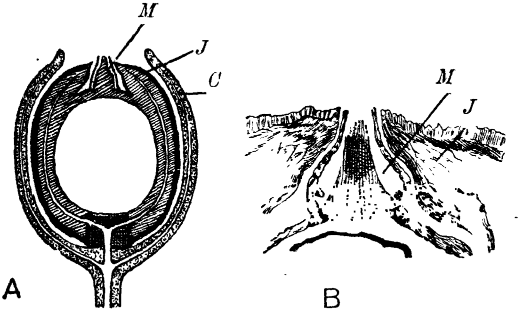


FIG. 528.—*Lyginodendron* macrosporangium. *A*, Diagrammatic longitudinal section. *B*, Longitudinal section of the upper portion. (× 25.) M, microspore-chamber; J, integument; C, cupule.

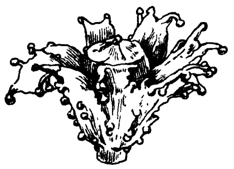


FIG. 529.—*Lyginodendron oldhamianum.* Macrosporangium (*Lagenostoma*). The open cupule bears stalked glands. Reconstruction. (After SCOTT, from ENGLER-PRANTL.)

The HAPLOID GAMETOPHYTE does not attain any higher differentiation than that of a thallus, and soon comes to the end of its development with the formation of ANTHERIDIA and ARCHEGONIA that are simpler in construction than those of the Bryophyta. In the heterosporous forms indeed there is no independently living gametophyte, for the prothallus, consisting of relatively few cells, remains more or less enclosed within the spore. The reduction is extreme in the case of the male gametophytes which remain enclosed by the spore-walls, and consist of a single vegetative cell bearing a single antheridium; only the small number of spermatozoids that are formed escape from the spore. The female prothalli, though composed of a larger number of cells, are also greatly reduced; their whole tissue is enclosed by the wall of the spore, from which the embryo, developed as a result of fertilisation, emerges. In some cases this reduction of the sexual generation is emphasised by the macrospore not escaping from the macrosporangium; and in extreme cases the macrosporangium being more closely attached to the sporophyte by the development of an integument, fertilisation and even the germination of the new sporophyte may thus take place on the parent plant.

All these relations in the Pteridophyta lead so clearly to the condition found in the Spermatophyta that it is difficult to draw a line between the two groups. Thus the Pteridosperms, included here among Pteridophyta, may alternatively be regarded as true Gymnosperms.

Within the various classes of the Pteridophyta HETEROSPORY has originated independently several times, as has also "seed-formation." A further development to higher plants has only taken place in the case of the Pteridosperms, which on the other side exhibit connections with the Eusporangiatae; the corresponding Lepidodendrales, on the other hand, appear to have ended blindly.

The lower phylogenetic connection of the Pteridophyta is less clear. In spite of the resemblances in the sexual organs, a derivation from the Bryophyta does not seem possible, for it is difficult to see how the highly differentiated sporophyte in the Pteridophyta can have originated from the dependent sporogonium. We are therefore forced to assume that the Bryophyta and Pteridophyta represent two parallel branches of the phylogenetic tree, which have taken origin in some unknown way from the Algae; while the Bryophyta end blindly, the Pteridophyta have developed further as the Spermatophyta.

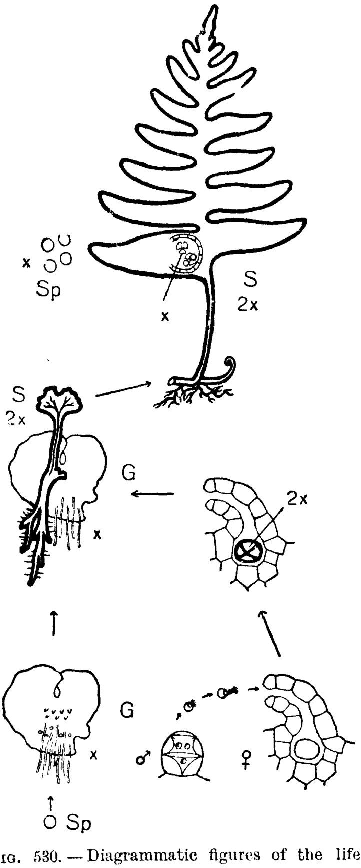


FIG. 530.—Diagrammatic figures of the life-history of a Fern. *G*, gametophyte; *S*, sporophyte; *Sp*, spore; *x*, haploid (thin lines); *2x*, diploid (thick lines).

The most primitive Pteridophyta are the Psilophytinae which appear in the Silurian, and thus earlier than any other Pteridophytes. In spite of the presence of true vascular bundles, their simplest leafless representatives, with sporangia terminating branches of the assimilating shoots, have a very "alga-like" habit. On the other hand, the forms with simple leaves connect, so far as habit is concerned, with the similarly small-leaved Lycopodiinae; they cannot be directly connected, however, since in the Lycopodiinae the sporangia are borne on sporophylls.

The various classes of Pteridophyta are somewhat loosely connected with one another. In particular, the forms with the small Lycopod-type of leaf are sharply distinguished from those with the large Fern-type of leaf. Probably all the classes are to be traced back as parallel lines to a common stock. The above arrangement of the classes does not therefore represent a phylogenetic succession.

Survey of the Classes of the Pteridophyta:

Psilophytinae. Leafless or with small leaves; sporangia terminal, not on leaves; isosporous.

Lycopodiinae. Leaves small; sporangia solitary on the upper surface of the sporophyll; isosporous or heterosporous; spermatozoids bi-ciliate. (Orders: Lycopodiales, Selaginellales, Lepidodendrales, see p. 515.)

Psilotinae. Leaves small; sporangia plurilocular, on the upper surface of the sporophyll; isosporous; spermatozoids multiciliate.

Equisetinae. Leaves small, in whorls; sporangia borne in numbers on the lower side of the sporophyll; isosporous or heterosporous; spermatozoids multiciliate. (Orders: Equisetales, Sphenophyllales, see p. 520.)

Isoëtinae. Leaves large relatively to the stem; sporangia solitary on the upper surface of the sporophyll; heterosporous; spermatozoids multiciliate.

Filicinae. Leaves large; sporangia numerous on the under side of the leaves; spermatozoids multiciliate.

Sub-class *Eusporangiatae.* Sporangial wall firm; isosporous.
Sub-class *Leptosporangiatae.* Sporangial wall thin; isosporous.
Sub-class *Hydropterideae.* Sporangial wall thin; heterosporous.

Pteridospermae. Leaves large; heterosporous; microsporangia numerous on the lower side of the sporophyll; macrosporangium with only one macrospore, which is not shed from the sporangium ("ovule").

Survey of the Spore-Plants (Thallophyta, Bryophyta, Pteridophyta)

The relationships of these plants are in many points obscure, as has been seen in the sections dealing with the various groups. A phylogenetic tree is given in Fig. 531. The black lines indicate relationships which may be assumed with some certainty; the dotted lines others that are doubtful. Where several lines are given they indicate alternative possibilities. Where no connections are indicated the relation of the class to others is still quite obscure.

As the diagram shows, the majority of the classes may be derived directly or indirectly from the Flagellatae. This appears most clearly from the organisation of the reproductive cells; both asexual swarm-spores and gametes are in many cases ciliated naked protoplasts of a Flagellate type. In the Bryophyta and

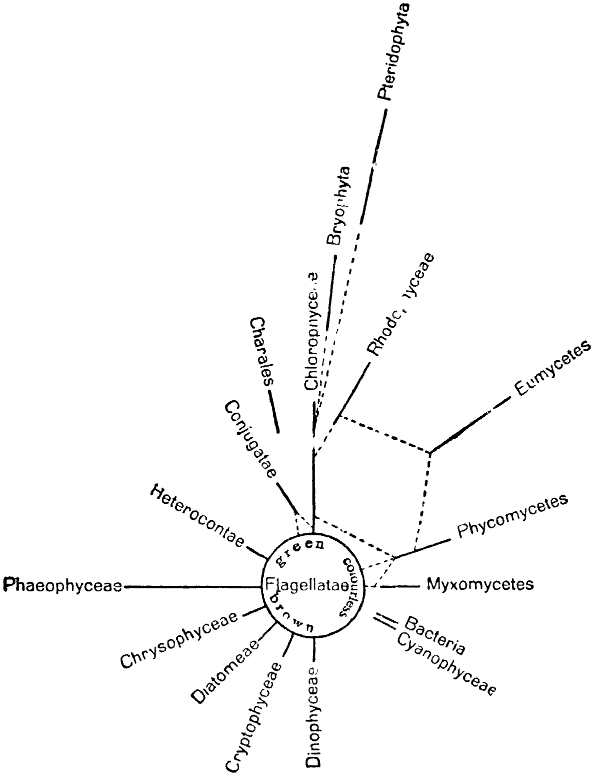


FIG. 531.—Diagrammatic representation of the interrelationships of Thallophyta, Bryophyta, and Pteridophyta. Explanation in text.

Pteridophyta, and even in the Cycadeae and Ginkgoaceae, this is seen in the case of the male gametes; though these are secondarily modified, their ontogeny indicates the phylogenetic original form.

DIVISION II

SPERMATOPHYTA

DIVISION II

SPERMATOPHYTA

The Transition from the Pteridophyta to the Spermatophyta (1).—The Pteridophyta are characterised by the type of alternation of generations they exhibit. The spore gives rise to the independently living, haploid gametophyte. This is the short-lived prothallus, from the fertilised egg-cell of which the physiologically independent diploid sporophyte arises and forms the Fern, Horse-tail, or Club-moss. The appearance of heterospory leads to a further reduction of the prothallus, which ceases to produce both kinds of sexual organs. In the germination of the microspores only a single, vegetative prothallium-cell is to be recognised, the remainder of the small prothallium representing one or more antheridia. The female prothallium, which in *Salvinia* still becomes green and emerges from the macrospore, in *Selaginella* and *Isoëtes* has lost the power of independent nutrition. The prothallium begins its development while still within the macrosporangium of the parent plant, and the macrospore, after being set free, only opens in order to allow of the access of the spermatozoids to the archegonia. From the fertilised egg, the embryo develops without a resting period into the young sporophyte.

The simplest Spermatophyta are only distinguished by inessential differences from these most highly differentiated Archegoniatae.

The MACROSPORE, which in the Spermatophyta is termed the EMBRYO-SAC, remains enclosed in the MACROSPORANGIUM or OVULE (Fig. 532). The latter consists of the NUCELLUS (*n*), from the base of which (the CHALAZA (*ch*)) one or two INTEGUMENTS (*ii*, *ia*) arise; these grow up as tubular investments of the nucellus and only leave a small passage, the MICROPYLE (*m*), leading to the tip of the latter. The ovule is attached to the MACRO-SPOROPHYLL or CARPEL by a stalk or FUNICULUS (*f*), which is often very short. The region to which one or more ovules are attached is called the PLACENTA. If the nucellus forms the direct continuation of the funiculus the ovule is termed straight or ATROPOUS. More frequently the funiculus is sharply curved just below the chalaza, so that the ovule is bent back alongside its stalk (ANATROPOUS ovule). The line of junction of the funiculus *with the outer integument is still recognisable in the ripe seed, and* is termed the RAPHE. Lastly the ovule itself may be curved, in which case it is spoken of as CAMPYLOTROPOUS. The three types are diagrammatically represented in Fig. 532 *A-C*.

As a rule only one embryo-sac is contained in an ovule. In the same way as the four macrospores originate by the tetrad division in the macrosporangium of *Selaginella*, in the macrosporangium (ovule) of the Spermatophyta there is usually a single embryo-sac mother-cell which divides into four daughter cells; three of these do not develop further, while the fourth becomes the embryo-sac. The embryo-sac of the simplest Spermatophyta also resembles the macrospore in becoming filled with prothallial tissue, here termed the endosperm; one or more archegonia with large egg-cells are developed at the summit of this. The fertilised ovum develops into the embryo while still enclosed within the macrospore and at the expense of the parent plant. When the embryo has reached a certain stage in its development, which is different and characteristic in different plants, its growth is arrested, and after the separation from the parent plant it undergoes a period of rest. It is still surrounded by the other portions of the macrosporangium, viz. the prothallium or endosperm, the nucellus (if this still persists), and the seed-coat formed from the integuments. THE COMPLETE STRUCTURE DERIVED FROM THE OVULE IS TERMED A SEED, AND THE FURTHER DEVELOPMENT OF THE UNOPENED MACROSPORANGIUM TO FORM A SEED IS CHARACTERISTIC OF ALL SEED-PLANTS OR SPERMATOPHYTA.

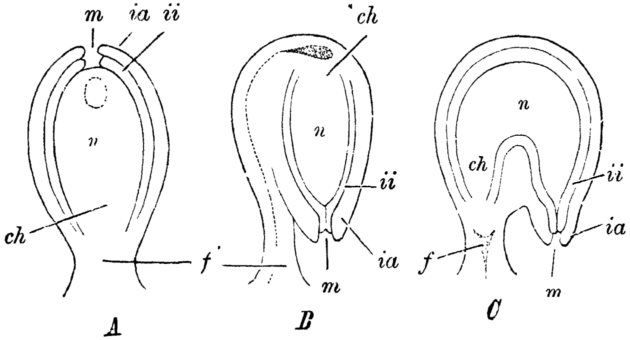


FIG. 532.—*A*, Atropous ; *B*, anatropous ; *C*, campylotropous ovules. Diagrammatic and magnified. Modified from SCHIMPER. Description in the text.

The MICROSPORES of the Spermatophyta are called POLLEN-GRAINS. They are formed in large numbers within the MICROSPORANGIA or POLLEN-SACS, which are borne singly or in numbers on the MICROSPOROPHYLLS or STAMENS. The part of the stamen which bears the pollen-sacs is usually clearly distinguishable and is called the ANTHER.

The development of the pollen-sac (Fig. 533) commences with divisions parallel to the surface taking place in cells of the hypodermal layer; this separates the cells of the primary archesporium from an outer layer of cells. The latter divides to form three layers of cells. The outermost layer of the wall in Gymnosperms and the hypodermal layer in the Angiosperms gives rise to the FIBROUS LAYER and the innermost layer to the TAPETUM. The archesporium, after undergoing a number of divisions, forms the pollen-mother-cells, each of which divides as in Bryophytes and Pteridophytes into four daughter-cells. These are the pollen-grains, and are spherical or ellipsoidal in shape and provided with a cell-wall, an external cutinised layer (the EXINE), and an inner cellulose layer, rich in pectic substances (the INTINE), can be distinguished in the wall.

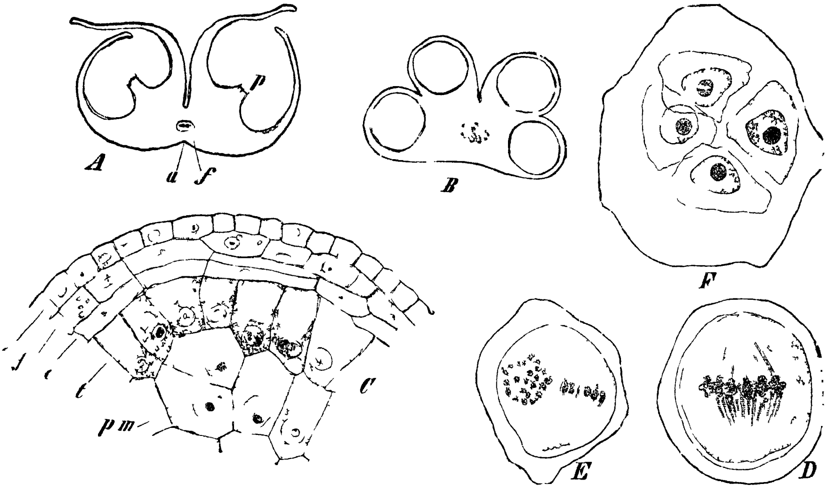


FIG 533 —*Hemerocallis fulva* *A*, Transverse section of an almost ripe anther, showing the loculi ruptured in cutting, *p*, partition wall between the loculi, *a*, groove in connective, *f*, vascular bundle (× 14) *B*, Transverse section of young anther (× 28) *C*, Part of transverse section of a pollen sac, *pm*, pollen mother cells, *t*, tapetal layer, later undergoing dissolution, *c*, intermediate parietal layer, becoming ultimately compressed and disorganised, *f*, parietal layer of eventually fibrous cells, *e*, epidermis (× 240). *D* and *E*, Pollen mother cells of *Alchemilla speciosa* in process of division (× 1125) *F*, Mature tetrad of *Bryonia dioica* (×800) (After STRASBURGER.)

While the male sexual cells of all archegoniate plants are dependent on water for their conveyance to the female organs, the transport of the pollen-grains to the egg-cells is brought about in Spermatophytes by means of the wind or by animals. However far the reduction of the male prothallium has proceeded—and even in the case of the heterosporous Pteridophyta only a single sterile cell was present—two constituent parts are always distinguishable in the germinating pollen-grain; these are a VEGETATIVE CELL which grows out as the

POLLEN-TUBE, and an ANTHERIDIAL CELL which ultimately gives rise to two GENERATIVE CELLS. The pollen-tube, the wall of which is continuous with the intine of the pollen-grain, ruptures the exine and penetrates, owing to its chemotropic irritability, into the tissue of the macrosporangium (cf. p. 355). The antheridial cell passes into the pollen-tube and sooner or later gives rise to two generative cells which reach the embryo-sac and egg-cell by passing along the pollen-tube. The name Siphonogams has been applied to the seed-plants on account of the common character of the group afforded by the formation of a pollen-tube.

The results reached by the above survey may be summarised by saying that the Phanerogams continue the series of the Archegoniatae and agree with the latter in exhibiting an alternation of generations (cf. the Scheme on p. 552). While the sporophyte becomes more complex in form and more highly organised, there is a corresponding reduction of the gametophyte. The female sexual generation is enclosed, throughout its whole development, in the asexual plant, and only becomes separated from the latter in the seed, which further contains as the embryo the commencement of the succeeding asexual generation.

The investigations made of recent years into the phenomena of the reduction-division (cf. p. 189) in the spore-mother-cells of Archegoniates and Spermatophyta have resulted in a confirmation of the limits of the two generations in the latter ([2]). The number of chromosomes characteristic of any plant is diminished to one-half, during the divisions that lead to the origin of the sexual generation, and the full number of chromosomes is not again attained until fertilisation takes place. The asexual generation has always the double number, the sexual generation the single number of chromosomes. The gametophyte is haploid, the sporophyte diploid.

The Spermatophyta are divided into two classes which differ in their whole construction: (1) THE GYMNOSPERMS, WITH NAKED SEEDS; (2) THE ANGIOSPERMS, WITH SEEDS ENCLOSED IN AN OVARY. THE CARPELS OF THE ANGIOSPERMS FORM A CLOSED CAVITY, THE OVARY, WITHIN WHICH THE OVULES DEVELOP. SUCH AN OVARY IS WANTING IN THE GYMNOSPERMS, THE OVULES OF WHICH ARE BORNE FREELY EXPOSED ON THE UPPER SURFACE OR MARGINS OF THE MACROSPOROPHYLLS OR CARPELS.

The Gymnosperms are the phylogenetically older group. Their construction is simpler and in the relations of their sexual generation they connect directly with the heterosporous Archegoniatae.

The Angiosperms exhibit a much wider range in their morphological and anatomical structure. The course of their life-history differs considerably from that of the Gymnosperms, and without the intermediate links supplied by the latter group the correspondence with the life-history of the Archegoniatae would not be so clearly recognisable.

These conclusions are confirmed by the evidence afforded by Palaeobotany. Gymnosperms or forms resembling them are found, along with what appear to be intermediate forms between the Gymnosperms and the Pteridophyta, in the fossiliferous rocks of the Devonian, Carboniferous, and Permian formations. The Angiosperms are, on the other hand, first known with certainty from the Cretaceous formation.

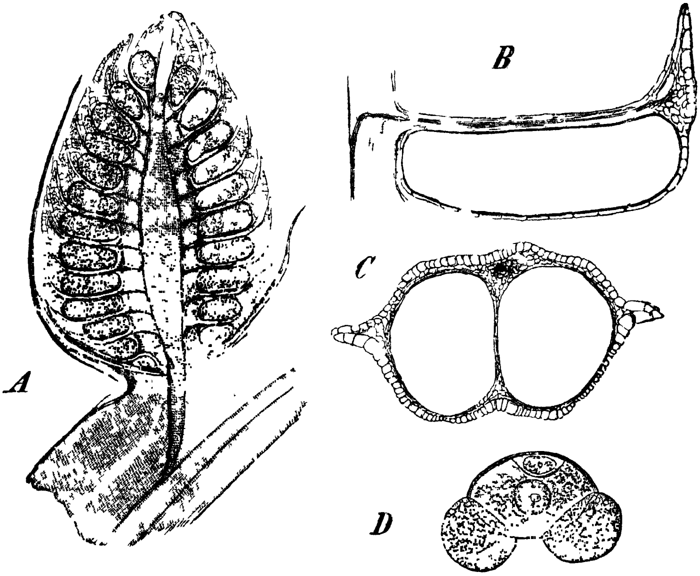


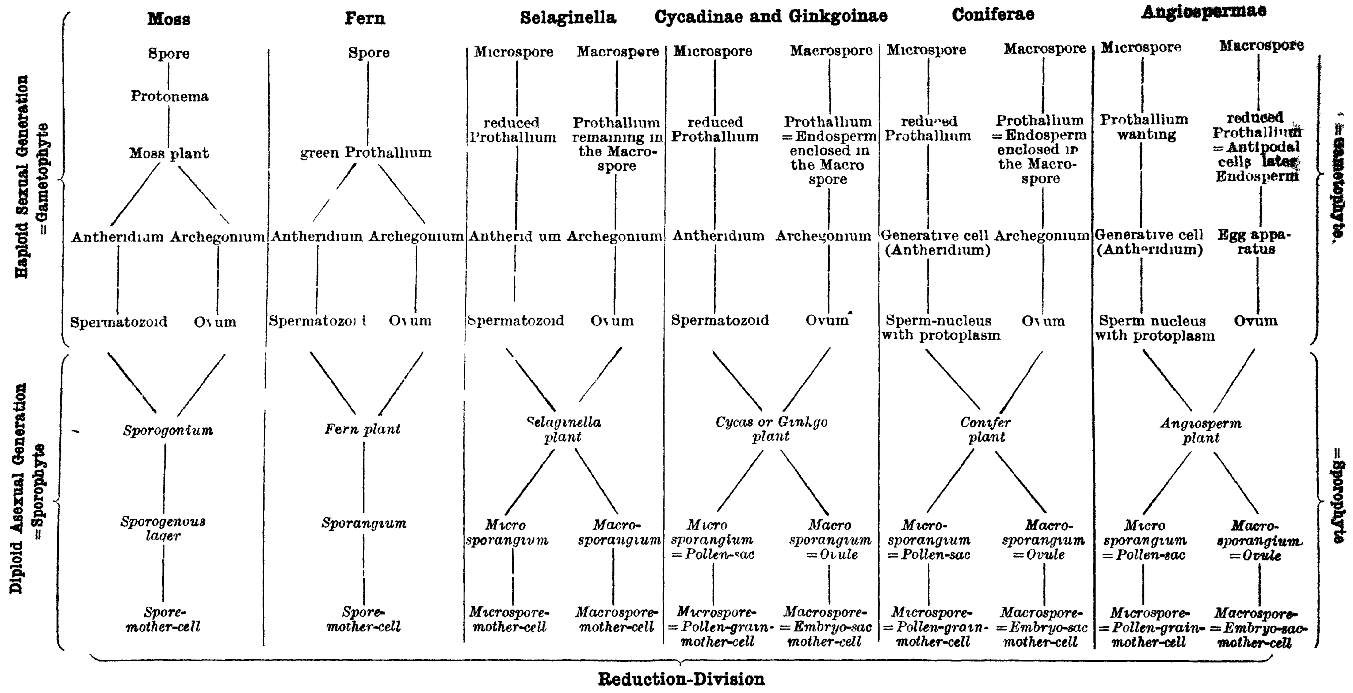
FIG 534 —*Pinus montana* *A*, Longitudinal section of a ripe male flower (× 10) *B*, Longitudinal section of a single stamen (× 20) *C*, Transverse section of a stamen (× 27) *D*, A ripe pollen-grain of *Pinus sylvestris* (× 400) (After STRASBURGER)

Morphology and Ecology of the Flower (1, 3)

1. **Morphology.**—The flowers of the **Gymnosperms** are all unisexual and diclinous. The macrosporophylls form the female, the microsporophylls the male flowers. The two sexes are found either on the same individual (MONOECIOUS), or each plant bears either male or female flowers (DIOECIOUS). Leaves forming an envelope around the group of sporophylls are only found in the Gnetaceae in the group of Gymnosperms.

The MALE FLOWERS of Gymnosperms are shoots of limited length, the axis of which bears the closely crowded and usually spirally arranged sporophylls. The scales which invested the flower in the bud often persist at the base of the axis (Fig. 534).

Scheme of Alternation of Generations



The microsporangia are borne on the lower surface of the sporophylls, two or more being present on each. Their opening is determined as in the sporangia of the Pteridophyta by the peculiar construction of the outer layer of cells of the wall (exothecium). The pollen-grains are spherical, and are frequently provided with two sacs filled with air, which increase their buoyancy and assist in their distribution by the wind (Fig. 534, *A-D*). On germination the outer firm layer of the wall of the pollen-grain (exine) is completely lost, being fractured by the increase in size of the protoplasmic body.

In many Gymnosperms the FEMALE FLOWERS or CONES resemble the male flowers in being composed of an axis bearing numerous spirally-arranged sporophylls. In other cases they differ from this type in various ways, which will be described below (pp. 604 ff.).

In **Angiosperms**, on the other hand, a union of micro- and macro-sporophylls in the one flower, which is thus HERMAPHRODITE, and the investment of the flower by coloured leaves (differing in appearance from the foliage leaves), forming a PERIANTH, is the rule (Figs. 535, 536). In contrast to the UNISEXUAL or DICLINOUS flower with the sporophylls arranged spirally on an elongated axis, which is characteristic of the Gymnosperms, the perianth-leaves and sporophylls in the Angiosperms are usually borne in whorls on a greatly shortened axis. THE ARRANGEMENT OF THE FLORAL LEAVES IN WHORLS, THE COLOURED PERIANTH, AND THE HERMAPHRODITE NATURE OF THE FLOWERS ARE THUS CHARACTERISTIC OF ANGIOSPERMS, although these features do not apply without exceptions to all angiospermic flowers. These differences depend on the important factor of the MEANS OF POLLINATION. When this function is performed by the wind, the elongation of the axis and the absence of an investment of leaves around the female receptive organ are advantageous. When, on the other hand, pollination is effected by insects or birds,

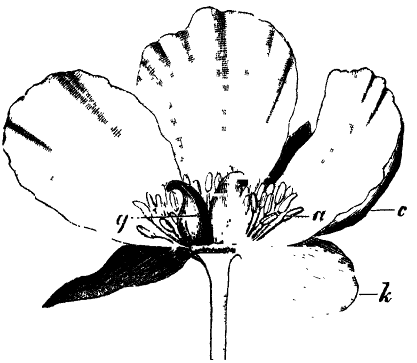


FIG. 535.—Flower of *Paeonia peregrina*. *k*, Calyx, and *c*, corolla, together forming the perianth; *a*, androecium; *g*, gynaeceum. The anterior portion of the perianth has been removed. (½ nat size. After SCHENCK.)

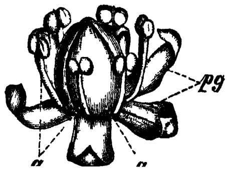


FIG. 536.—Flower of *Acorus Calamus*. *pg*, Perigone; *a*, androecium; *g*, gynaeceum. (Enlarged. After ENGLER.)

the conspicuousness given by the presence of a perianth and other attractions, such as scent or sweet-tasting substances, are necessary. The form of the flower, the arrangement of the sporophylls in it, and the place at which nectar is secreted must be adapted to the body-form or the habits of the visiting animals. It is to this that the variety of form and colour exhibited in the flowers of Angiosperms must be ascribed.

The association of hermaphrodite and unisexual flowers on the same plant leads in certain Angiosperms to what is known as POLYGAMY. When hermaphrodite and unisexual flowers are distributed on distinct individuals we have andro- or gyno-dioecism; when on the same individual andro- or gyno-monoecism.

The perianth usually consists of two whorls of members: these may be similar in form and colour (*e.g. Lilium*), when the name PERIGONE is given to them, or may be differentiated into an outer green CALYX and an inner whorl of coloured leaves, the COROLLA (*e.g. Rosa*). In every complete flower two whorls of stamens or microsporophylls come next within the perianth, and within these again a whorl of carpels or macrosporophylls. The whorls alternate regularly with one another. The stamens collectively form the ANDROECIUM, the carpels the GYNAECEUM.

Each stamen consists of a cylindrical stalk or FILAMENT and of the ANTHER; the latter is formed of two THECAE or pairs of pollen-sacs joined by the continuation of the filament, the CONNECTIVE (Fig. 537). According to whether the thecae are turned inwards, *i.e.* towards the whorl of carpels, or outwards, the anther is described as INTRORSE or EXTRORSE. The opening of the ripe theca depends as a rule (except in the Ericaceae) on the peculiar construction of the hypodermal layer of the wall of the pollen-sac. This is called the FIBROUS LAYER or ENDOTHECIUM. On the other hand, in the Gymnosperms (excluding *Ginkgo*, cf. p. 604), as in the Ferns, the dehiscence is effected by means of the external layer of cells (EXOTHECIUM). As a rule the septum between the two pollen-sacs breaks down, so that they are both opened by the one split in the wall (Fig. 533 *A*). The microspores in anemophilous plants are smooth, dry, and light, and adapted for distribution by the wind. In entomophilous flowers, on the other hand, the exine is frequently sticky or provided with spiny projections, and the pollen-grains are thus enabled to attach themselves better to the bodies of the insect visitors. They also differ from the pollen-grains of the Gymnosperms in not losing the exine on germination, but having more or less numerous spots in the wall prepared beforehand for the emission of the pollen-tube (Fig. 538). Sterile stamens which do not produce fertile pollen are termed STAMINODES (cf. *e.g.* the Scitamineae).

The flower is terminated above by the GYNAECEUM. The CARPELS composing this may remain free and each give rise to a separate fruit

(APOCARPOUS GYNAECEUM) (Figs. 539, 542 *A*), or they unite together to form the ovary (SYNCARPOUS GYNAECEUM) (Fig. 540). The

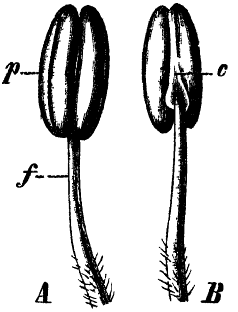


FIG 537 —*A* and *B*, Anterior and posterior view of a stamen of *Hyoscyamus niger*, *f*, the filament, *p*, anther, *c*, connective (magnified) (After SCHIMPER.)

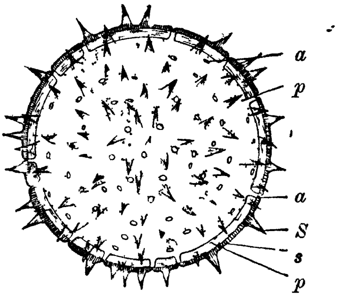


FIG 538 —Pollen grain of *Malva sylvestris*. *S*, Spinous projections of the exine, *s*, vertically striated layer of the exine, *p*, the same seen from above, *a*, places of exit of pollen-tubes. (After A. MEYER.)

carpels, as a rule, bear the ovules on their margins, on more or less evident outgrowths which are termed PLACENTAS (Fig. 539 *p*). In apocarpous gynaecea the ovules are thus borne on the united margins of the carpels, each margin bearing a row of ovules. This is termed the VENTRAL SUTURE, while the midrib of the carpel forms the DORSAL SUTURE. In syncarpous ovaries the ovules are similarly borne on the margins of the coherent carpels (Fig. 541 *pl*).

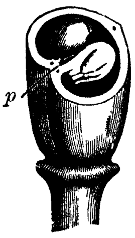


FIG. 539 —*Delphinium consolida*. Cross-section of the ovary, showing the ovules on the placenta (*p*). (After ENGLER-PRANTL.)

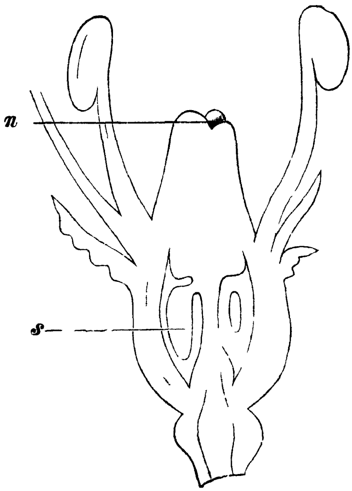


FIG. 540 —*Sambucus nigra*. Longitudinal section of flower *s*, Ovule; *n*, stigma. (After TSCHIRCH-ÖSTERLE.)

The placentation is termed PARIETAL when the placentas form projections from the inner surface of the wall of the ovary (Fig. 541 *D*). If the margins of the carpels project farther into the ovary, and divide its cavity into chambers or loculi, the placentas are correspondingly altered in position, and the placentation becomes AXILE (Fig. 541 *B*). In contrast to such TRUE SEPTA, formed of the marginal portions of the carpels, those that arise as outgrowths of the surface or sutures of the carpels, as in the Cruciferae, are called FALSE SEPTA (Fig. 683) By

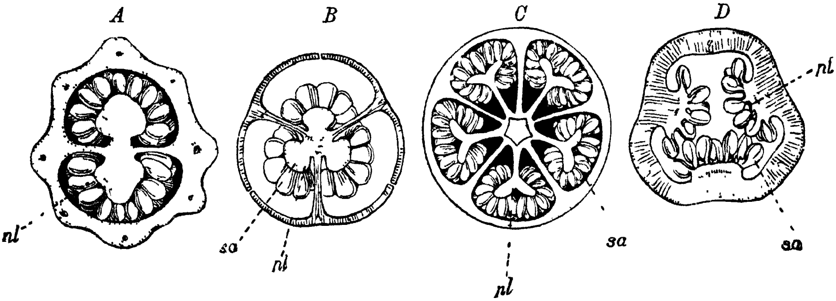


FIG. 541 —Transverse sections of ovaries *A*, *Lobelia* *B*, *Diapensia*, *C*, *Rhododendron*, *D*, *Passiflora*, *pl*, placenta, *sa*, ovules (After LE MAOUT and DECAISNE)

the upgrowth of the floral axis in the centre of the ovary what is known as FREE CENTRAL PLACENTATION comes about (*e g*. Primulaceae). The projecting axis cannot be sharply distinguished from the tissue of the carpels. The septa, which were originally present, are arrested at an early stage of development or completely disappear, so that the ovules are borne on the central axis covered with carpellary tissue and enclosed in a wall formed by the outer portions of the carpels.

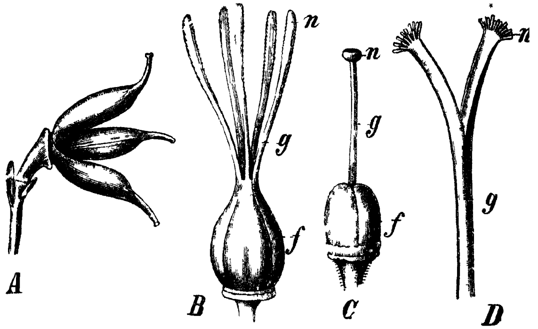


FIG 542 —Different forms of gynaecea *A* Of *Aconitum Napellus*, *B*, of *Linum usitatissimum*, *C*, of *Nicotiana rustica*, *D*, style and stigma of *Achillea millefolium*; *f*, ovary, *g*, style, *n*, stigma (After BERG and SCHMIDT, magnified)

Each carpel in an apocarpous gynaeceum is usually prolonged above into a stalk-like STYLE terminating in a variously-shaped STIGMA. The stigma serves as the receptive apparatus for the pollen, and in relation to this is often papillate or moist and sticky (Fig. 542 *D*). When the gynaeceum is completely syncarpous, it has only one style and stigma. In Fig. 542 an apocarpous (*A*) and a syncarpous gynaeceum

(*C*) are represented, together with one in which the carpels are coherent below to form the ovary while the styles are free (*B*).

The POSITION OF THE OVULES WITHIN THE OVARY may be erect, pendulous, horizontal, or oblique to the longer axis (Figs. 543, 544). In anatropous ovules the raphe is said to be ventral when it is turned towards the ventral side of the carpel, and dorsal if towards the dorsal side of the carpel.

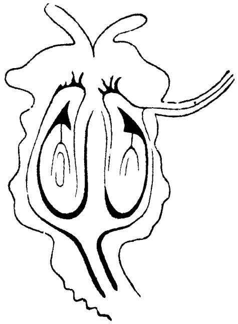


FIG. 543.—Ovary of *Conium maculatum* with pendulous ovules, in longitudinal section Raphe ventral. (After TSCHIRCH OSTERLE)

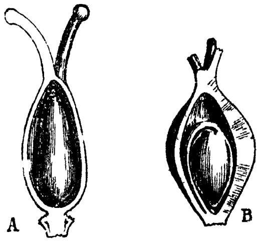


FIG 544 —Ovaries containing basal ovules shown in longitudinal section A, *Fagopyrum esculentum* (atropous), B, *Armeria maritima* (anatropous) (× 20 After DUCHARTRE)

The differences in the form of the FLORAL AXIS, which involve changes in the position of the gynaeceum, lead to differences in the form of the flower itself Some of the commonest cases are diagrammatically represented in Fig. 545 *A*-*C*. The summit of the floral axis is usually thicker than the stalk-like portion below; it is often widened out and projecting, or it may be depressed and form a cavity. If the whorls of members of the flower are situated above one another on a simple, conical axis, THE GYNAECEUM FORMS THE UPPERMOST WHORL AND IS SPOKEN OF AS SUPERIOR, WHILE THE FLOWER IS TERMED HYPOGYNOUS (Fig. 546, 1). If, however, the end of the axis is expanded into a flat or cup-shaped receptacle (hypanthium), an interval

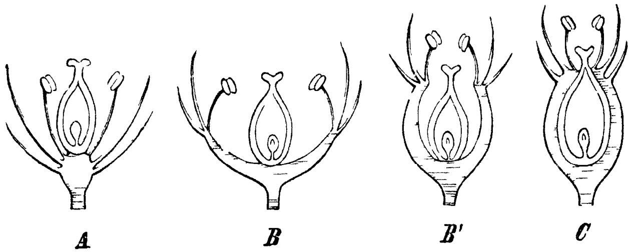


FIG 545 —Diagram of (*A*) hypogynous, (*B*, *B′*) perigynous, and (*C*) epigynous flowers. (After SCHIMPER.)

thus separating the androecium and gynaeceum, the flower is termed PERIGYNOUS (Figs. 545 *B*, *B′*, 546, 2). When the concave floral axis, the margin of which bears the androecium, becomes adherent to the gynaeceum, the latter is said to be INFERIOR, while the flower is described as EPIGYNOUS (Fig. 546, 3).

The regions of the axis, or of other parts of the flower which excrete a sugary solution to attract the pollinating animal visitors, are called NECTARIES. Their ecological importance is considerable.

In a typical angiospermic flower the organs are thus arranged in five alternating whorls, of which two comprise the perianth, two the androecium, while the gynaeceum consists of one whorl. The flower is PENTACYCLIC. The number of members is either the same in each whorl (*e.g.* three in a typical Monocotyledon flower, or five in a typical Dicotyledon flower), or an increase or decrease in the number takes place. This is especially the case with the whorls composing the androecium and gynaeceum. Further, as is shown in the androecium, a whorl may be entirely omitted or the number of whorls may be increased. Flowers with only one whorl in the androecium are termed HAPLOSTEMONOUS, and those with two whorls DIPLOSTEMONOUS. When the outer whorl of the androecium (and in correspondence with this the carpels) does not alternate with the corolla but falls directly above this, the androecium is OBDIPLOSTEMONOUS.

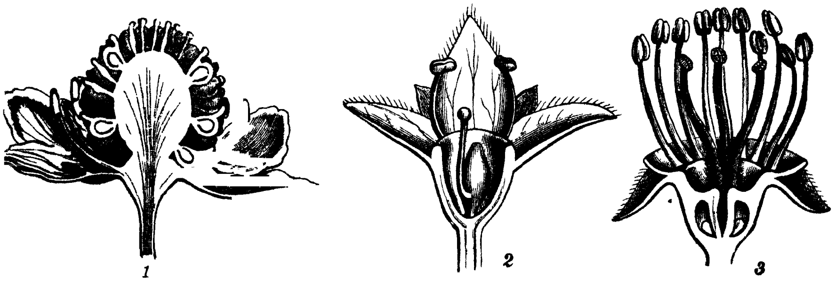


FIG. 546.—Flowers in longitudinal section 1, *Ranunculus sceleratus* with numerous apocarpous carpels on a club-shaped receptacle; hypogynous flower. (After BAILLON, magnified.) 2, *Alchemilla alpina*, perigynous; 3, *Pyrus Malus*, epigynous. (After FOCKE in *Nat Pflanzenfamilien*, magnified.)

A diagram (cf. p. 84) of a pentacyclic Monocotyledon flower, so oriented that the cross-section of the axis of the inflorescence stands above and that of the subtending bract (cf. p. 117) below, is given in Fig. 547, and that of a Dicotyledon flower in Fig. 548.

Both these floral diagrams are spoken of as EMPIRICAL DIAGRAMS. A THEORETICAL DIAGRAM, on the other hand, is obtained when not only the organs actually present are represented but also others the former presence of which must be assumed on phylogenetic grounds. Thus in the Iridaceae, which are closely related to the Liliaceae, only one whorl of stamens (the outer) is present; the inner whorl which might have been expected has been lost. When the position of the missing members is marked by crosses in the empirical diagram the theoretical floral diagram of the Iridaceae is obtained (Fig. 549). Occasionally "complete" flowers of *Iris* are met with corresponding to the theoretical diagram. HEINRICHER (4) has succeeded in propagating this floral form by seed. Such a reversion to ancestral characters is termed "atavism" (cf. p 194).

A FLORAL FORMULA gives a short expression for the members of a flower as shown in the floral diagram. Denoting the calyx by K, the corolla by C (if the perianth forms a perigone it is denoted by P), the androecium by A, and the gynaeceum by G, the number of members in each case is placed after the letter. When there is a large number of members in a whorl the symbol ∞ is used, denoting that the number is large or indefinite. Such a formula may be further made to denote the cohesion of the members of a whorl by enclosing the proper number within brackets; by placing a horizontal line below or above the number of the carpels the superior or inferior position of the ovary is expressed.

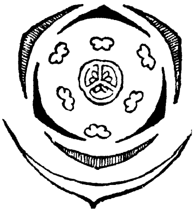


FIG. 547.—Diagram of a pentacyclic monocotyledonous flower (*Lilium*). (After SCHENCK.)

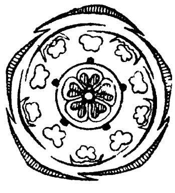


FIG. 548.—Diagram of a pentacyclic dicotyledonous flower (*Viscaria*). (After EICHLER.)

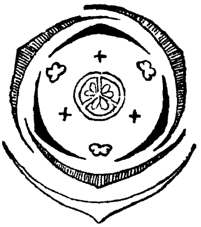


FIG. 549.—Theoretical diagram of the flower of *Iris*. The missing whorl of stamens is indicated by crosses (After SCHENCK.)

The floral diagrams in Figs. 547 and 548 would be expressed respectively by the floral formulae, P3+3, A3+3, G(3) for the Monocotyledon, and K5, C5, A5+5, G(5) for the Dicotyledon. Other examples are *Ranunculus*, K5, C5, A∞, $G\underline{\infty}$; Hemlock, K5, C5, A5, $G(\overline{2})$; *Artemisia*, K0, C(5), A(5), $G(\overline{2})$.

By displacement of the floral members, by inequalities in their size, or by the suppression of some of them, the original radial (actinomorphic) construction (Fig. 551 *A*) is modified; either dorsiventral (zygomorphic) flowers (Fig. 551 *B*) or completely asymmetrical flowers (Fig. 551 *C*) may result. In the floral formula ⊕ indicates an actinomorphic and ↓ a zygomorphic flower, *e.g.* Laburnum, ↓ K5, C5, A (5 + 5), $G\underline{1}$. Zygomorphic flowers always tend to assume a definite position in relation to the vertical. Radial monstrosities of normally dorsiventral flowers are termed peloric.

Inflorescences.

The flowers of Angiosperms stand singly in relatively few cases. They are much more commonly grouped in smaller or larger numbers on special branch-systems which are termed INFLORESCENCES. These contrast with vegetative branch-systems by the crowded position of their lateral branches, the usual development as scale-leaves of the subtending leaves or bracts, in the axils of which the lateral branches or the individual flowers stand, and by the development, in many cases at least, of all the axillary buds. In the case of the inflorescences of the Cruciferae, bracts are completely wanting.

FIG 550 —Atavistic form of *Iris pallida* Lam, *abavia* (After E HEINRICHER)

A THE MAIN AXIS GROWS MORE STRONGLY THAN THE LATERAL AXES

Inflorescences, like vegetative branch systems, may be monopodial (cf. p. 22), the main axis growing more actively than its lateral branches, or at least as actively ; such RACEMOSE INFLORESCENCES exhibit various forms (cf. diagrams, Fig. 552)

(*a*) Lateral axes unbranched.

1 RACEME stalked flowers borne on an elongated main axis (Fig. 552 *A*, Fig 555).

2 SPIKE flowers sessile on an elongated main axis (Fig. 552 *B*, Fig. 553). A spike in which the axis is thickened and succulent is termed a SPADIX : a spike which, after flowering or after the fruits have ripened, falls off as a whole is a CATKIN (Fig. 554).

3. UMBEL: a number of lateral axes bearing flowers on a main axis which grows to the same length and ends in a flower (Fig. 552 *C*, Fig. 556).
4. CAPITULUM or HEAD: flowers sessile on a shortened, and often broadened, main axis (Fig. 552 *D* (Compositae) Fig. 818).

(*b*) Lateral axes branched.

1. PANICLE: an elongated main axis bearing racemes laterally (Fig. 552 *E*, Fig. 557).
2. COMPOUND UMBEL: an umbel which has small umbels in place of the single flowers (Fig. 552 *F*, Fig. 756).

B. THE MAIN AXIS GROWS LESS STRONGLY THAN THE LATERAL AXES

If the relative main axis is overtopped by the lateral axis each time, the inflorescence is CYMOSE. These cymose inflorescences can be divided according to the number and position of the lateral shoots into the PLEIOCHASIUM, DICHASIUM and MONOCHASIUM. These types of branching have already been described (p. 122), and represented in ground-plan (Fig. 148). There also the monochastal branch-systems, the DREPANIUM, and RHIPIDIUM, and also the BOSTRYX and CINCINNUS, derived from the dichasium, are sufficiently treated. It is only necessary here to represent a typical dichasium (Fig. 558) and a cincinnus (Fig. 559).

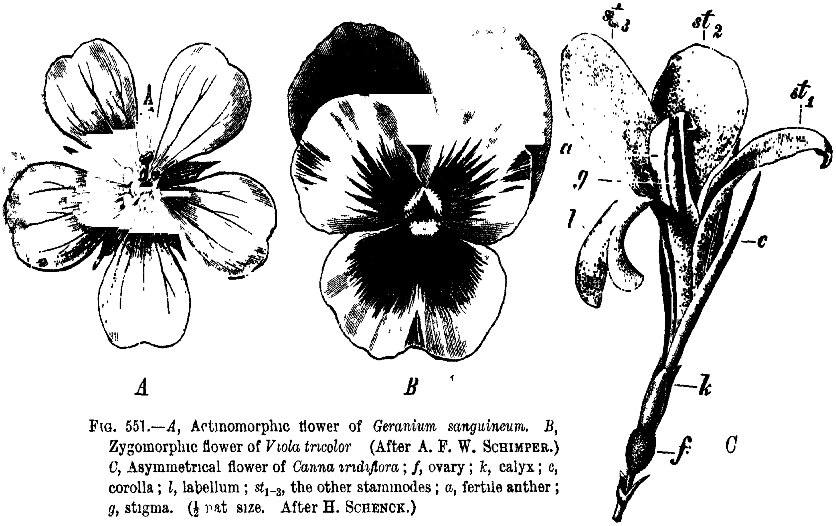


FIG. 551.—*A*, Actinomorphic flower of *Geranium sanguineum*. *B*, Zygomorphic flower of *Viola tricolor* (After A. F. W. SCHIMPER.) *C*, Asymmetrical flower of *Canna iridiflora*; *f*, ovary; *k*, calyx; *c*, corolla; *l*, labellum; st_{1-3}, the other staminodes; *a*, fertile anther; *g*, stigma. (½ nat size. After H. SCHENCK.)

2. Ecology. Pollination of Flowers (5) (cf. p. 188).—Many differences in the structure of flowers and in the arrangement of their organs which would otherwise be doubtful are explained when they are regarded ecologically. All flowers have the function of producing progeny sexually; the methods leading to this common end are, however, very various. In contrast to the Bryophyta and Pteridophyta in which the union of the sexual cells is effected by the aid of water, the Spermatophyta, which do not separate a motile male gamete, and have the egg-cells permanently enclosed in the tissues of the parent-plant, are forced to adopt other methods. Arrangements to convey the microspores, enclosing the male sexual cell, to the macrospores,

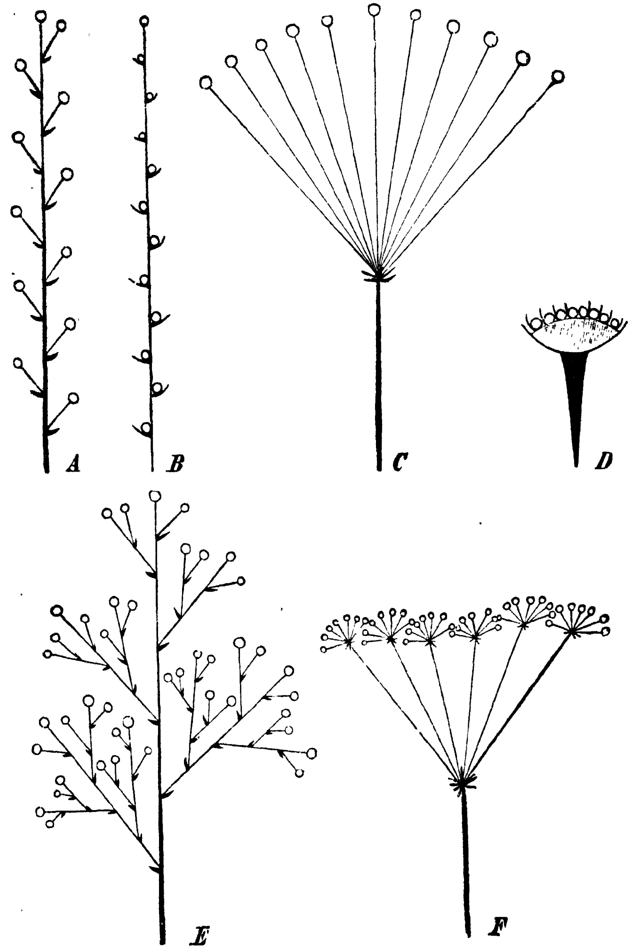


FIG. 552.—Diagrams of racemose inflorescences. *A*, Raceme. *B*, Spike. *C*, Umbel. *D*, Capitulum. *E*, Panicle. *F*, Compound umbel.

enclosed in the macrosporangia and containing the egg-cells, become necessary. In the first place the stigma (or micropyle), which is to receive the pollen, must be POLLINATED.

A large number of Spermatophyta make use of the wind to convey the microspores, *i.e.* the pollen, to its destination. Examples are all the Conifers, and also the majority of our native deciduous trees such as the Elm, Oak, Beech, Hornbeam, and further our Grasses and cereals. Simple as the relations in this case appear to be, various necessary preliminaries are required for successfully effecting this method of pollination.

It is especially necessary that such ANEMOPHILOUS plants should produce a very large quantity of pollen, since naturally only a small fraction of what is shed will reach its destination. Thus at the season when our coniferous woods are in flower, large quantities of pollen fall to the ground, constituting what are known as "sulphur showers."

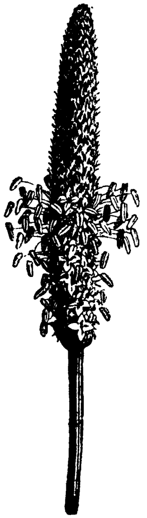


FIG. 553.—Spike of *Plantago lanceolata*. (After DUCHARTRE.)

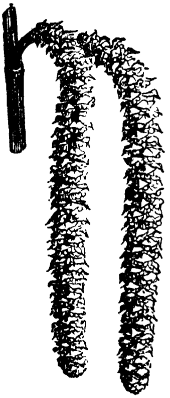


FIG. 554.—Catkin of *Corylus americana*. (After DUCHARTRE.)

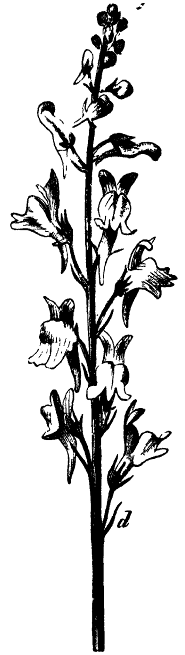


FIG. 555.—Raceme of *Linaria striata*. *d*, Bracts. (After A. F. W. SCHIMPER.)

Anemophilous plants exhibit some characters in common, which stand in definite relation to wind-pollination and cannot be regarded as merely accidental. The MALE INFLORESCENCE has usually the form of a longer or shorter catkin (Fig. 560) which bears a large number of microsporophylls; these are so oriented that after the sporangia have opened, the pollen can be readily carried away by the wind. Examples are the catkins of the Oak (Fig. 666), Birch (Fig. 660), Alder, Hazel, Hornbeam (Fig. 661), and Walnut; the catkins of the last-named plant (Fig. 658) are especially long. The male flowers of the Coniferae (Fig. 625) are similar. The mode of attachment of the anthers of Gramineae on long slender filaments has the same significance (Fig. 561). The pollen-grains of anemophilous flowers also have characteristic features. They are light and smooth, and in some Conifers are even provided with two wing-like sacs (Fig. 534 *D*), which enable them to remain suspended longer in the air. Some Urticaceae (*Pilea*, *Urtica*) scatter the pollen on the opening of the elastically-stretched wall of the pollen-sac as a light cloud of dust.

The **FEMALE FLOWERS** are usually not brightly coloured and do not develop nectaries. The stigmas, which catch the pollen, are strongly developed and provided with long feathery hairs (Fig. 561), or their form is brush-like, pinnate or elongated, and filamentous. In many Gymnosperms (*e.g. Taxus*) the micropyle of the macrosporangium excretes a drop of fluid in which the pollen-grains are caught; on drying up of the drop, the pollen is drawn down on to the tip of the nucellus. In other cases the pollen-grains glide down between the carpellary scales of the cones till they reach the moist micropyles of the ovules and adhere to them.

Lastly, the time of flowering is not without importance. The Elm flowers in February and March long before its leaves develop, and the same holds for the Hazel, Poplar, and Alder (Fig. 560). In the Walnut, Oak, Beech, and Birch, the flowers open when the first leaves are unfolding, and flowering is over before the foliage is fully expanded. Were this not so, much of the pollen would be intercepted by the foliage leaves, and even more pollen would need to be produced than has to be done to ensure fertilisation. In the Conifers the foliage presents less difficulty, but here the female cones are borne at the summit of the tree (*Abies*) or high up (*Picea*), while the male flowers are developed on lower branches. The pollen-grains are shed in warm dry weather, and carried up in the sunshine by ascending currents of air till they reach their destination on the female cones situated high above the male flowers.

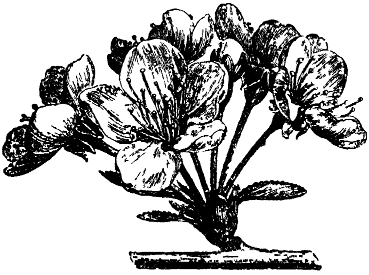


FIG. 556.—Umbel of the Cherry. (After DUCHARTRE.)

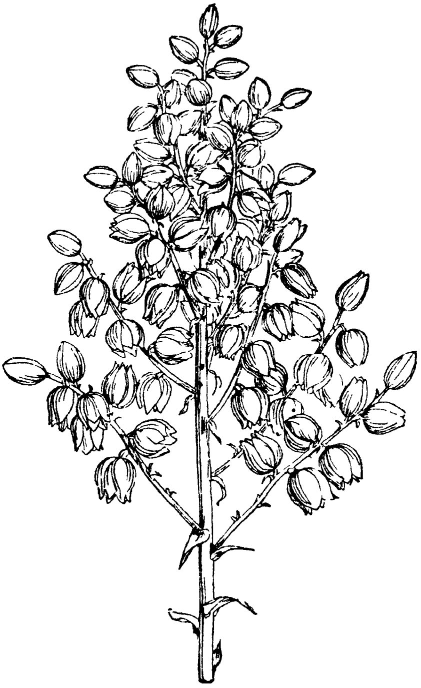


FIG. 557.—Panicle of *Yucca filamentosa*. (After A. F. W. SCHIMPER. Reduced.)

Only a small number of Phanerogams make use of the agency of water for effecting their pollination, and are, on that account, termed HYDROPHILOUS PLANTS. This applies only to submerged water-plants which do not emerge from the medium, *e.g. Zostera*, Seawrack, *Vallisneria spiralis* and *Elodea*.

The great majority of Phanerogams are dependent upon animals, especially on insects, for the transference of their pollen. Plants pollinated by the aid of insects are termed ENTOMOPHILOUS.

Since KONRAD SPRENGEL in his famous work, *Das entdeckte Geheimnis der Natur im Bau und in der Befruchtung der Blumen*, 1793, revealed the mutual relations between the forms and colours of flowers and the insects that frequent them, no other department of biology has been more actively studied than floral ecology. It is the more remarkable that no one had put the question whether the colours seen by our eyes were also perceived by the insects in the same way. It was difficult to think of the display of colour in meadow or orchard otherwise than as an apparatus of attraction for the visiting insects seeking the food provided by the nectaries of the flowers, although flowers which are not entomophilous may develop bright colours, *e.g.* Coniferae, stigmas of *Corylus*, etc.

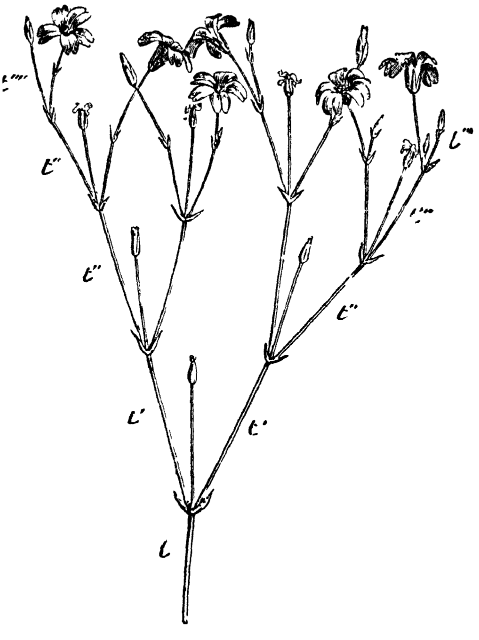


FIG. 558.—Cymose inflorescence (dichasium) of *Cerastium collinum*. t-t' , Successive axes. (After DUCHARTRE.)

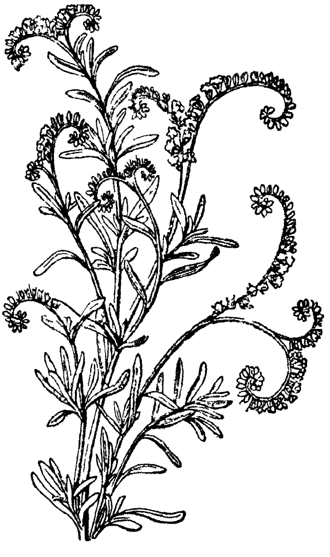


FIG. 559.—*Heliotropium Curassavicum*. Cincinnus. (After ENGLER-PRANTL.)

We owe the opening up of this question to C. HESS (6). He held that bees, the most important visitors to flowers, are colour-blind. This view has, however, been contradicted by the investigations of FRISCH, who has shown that we can at most assume colour-blindness for red and green in bees.

On more accurate investigation of the irritability of bees to various regions of the spectrum, KUHN and POHL (6) found that the wave-lengths and colours: 1, 650 - 500$\mu\mu$ orange, yellow, and yellowish-green; 2, 510 - 480$\mu\mu$ blue-green; 3, 470 – 400$\mu\mu$ bluish-violet; 4, 400 – 313$\mu\mu$ ultra-violet were distinguished qualitatively by bees.

By a series of careful experiments v. FRISCH (7) has established extremely interesting and intimate connections between bees and their visits to flowers. He distinguishes in this respect "searchers" and "collectors." The searchers discover new productive sources of nectar by means of the colours which they perceive at a considerable distance, and when closer recognise by their scent the most suitable flowers. They communicate their discoveries to their companions in the hive by means of characteristic signs and return with one or more collectors to thoroughly exploit the place. Fr. KNOLL has carried out a series of careful and critical observations on other important visitors to flowers; according to him (8) the Humble Bees (*Bombylius fuliginosus*) like the Bees are colour-blind to red and blue-green, and react like them to yellow and blue.

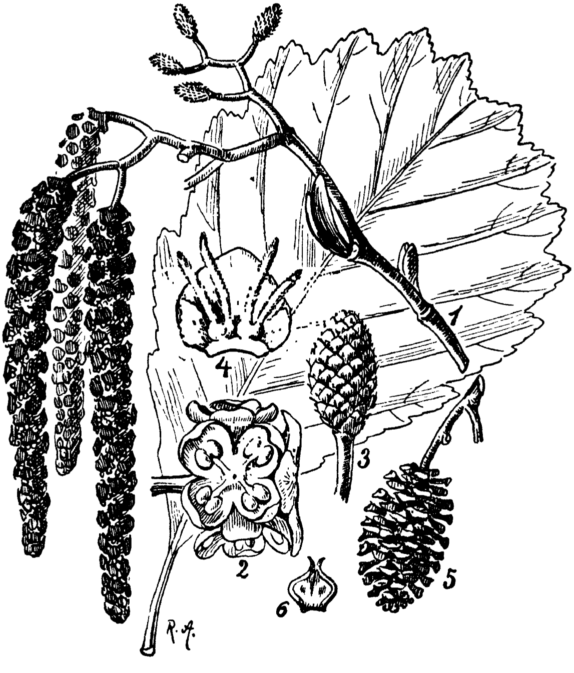


FIG. 560.—*Alnus glutinose.* *1*, Leaf and flowering twig with erect female and pendulous male catkins. *2*, Bract with male flowers. *3*, Female catkin. *4*, Two female flowers with bract. *5*, Fruiting catkin. *6*, Fruit. ($\frac{3}{4}$ natural size; 2-6 magnified.)

The researches of KNOLL on the Humming Bird Hawk Moth are of special interest. This is sensitive to contrasts, and in particular, dark is avoided. The significance of honey-guides as showing the way to the insect was studied by KNOLL by means of the marks made by the proboscis of moths on glass plates introduced into the flowers. In the attraction of moths it is the sense of sight and not of smell that is effective. Blue, violet, and purple form one group of perceptions, and yellowish-red another; an alteration of tone as regards the two is possible.

An orientation by sight is also found to hold for the Convolvulus Hawk Moth which flies in the late evening; it can discover darkly coloured (purple) flowers with certainty when it is so dark that a man at the normal visual distance can no longer distinguish them. The scent is in this case also not a means of orientation; it is possible in other cases to obtain results from the scent of flowers.

It is of interest to find that KNOLL discovered that the strong faecal odour of the inflorescence of *ARUM* attracted coprophilous insects, especially beetles and flies, from a distance. The inflorescence constitutes a trap. The epidermis of the spathe and spadix bears oily downwardly directed papillae, which are longest in region of the constricted neck; these afford no grip to the insects which slide into the lower chamber. On the withering of the papillae the insects are set free on the second day covered with pollen from the protogynous flowers (*cf.* dichogamy, p. 570).

While recent investigations have enriched and made more exact our knowledge on these points, the main facts demonstrated by SPRENGEL and those who followed him a hundred years later must not be forgotten. It is a matter of experience that plants which can be grown successfully away from their native countries may set no seed in the absence of the insect visitors to which they are adapted. An example is afforded by the Vanilla Orchid, which, away from its native country, Mexico, requires to be artificially pollinated. Such facts are so numerous that no doubt can be entertained as to the adaptedness of flowers to particular insects and conversely.

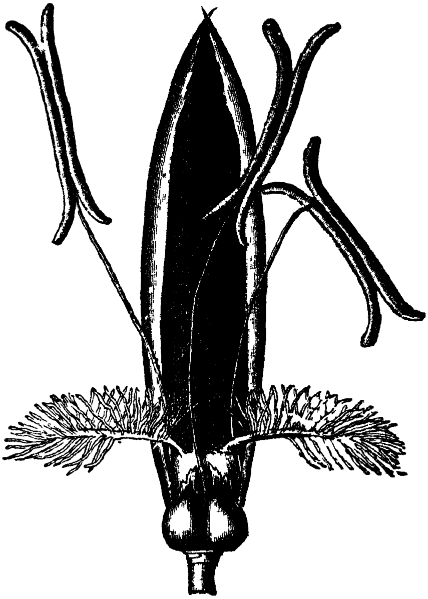


FIG. 561.—Anemophilous flower of *Festuca elatior*. (After SCHENCK.)

Usually the position of the nectaries is such that the hairy body of the visiting insect must carry away pollen from the flower; often the pollen will be deposited on special regions of the insect's body, and, when another flower is visited, will be deposited on the stigma. It is of importance that the pollen of such entomophilous plants differs from that of the anemophilous flowers described above. Pollen-grains provided with spiny projections, or with a rough or sticky surface, are characteristic of entomophilous plants · the grains may remain united in tetrads or in larger masses representing the contents of a whole pollen-sac (*Orchis*, Fig. 861, *Asclepias*, Fig. 775). The pollen itself forms a valuable nitrogenous food for some insects such as bees; these form "bee-bread" from it.

An example of a very close relation between floral construction and the body of the visiting insect, which was originally described by KONRAD SPRENGEL, is afforded by the pollination of *Salvia pratensis* by Humble Bees. Fig. 562, 1, shows a flower of *Salvia* with a Humble Bee on the lower lip in search of nectar. The flower has only two stamens, the two halves of each anther being quite differently developed, and separated by an elongated connective; the one half-anther is sterile and forms a projection in the throat of the corolla-tube, the other at the end of the long arm of the connective is fertile and lies beneath the hood formed by the upper lip of the corolla. The connective thus forms a lever, with unequal arms, movable on the summit of the short filament. When the bee introduces its proboscis, it presses on the short arm of the lever; the fertile half-anther is thus by the movement of the connective (*c*) on its place of attachment to the filament (*f*) brought down against the hairy dorsal surface of the insect's body (Fig. 562, 1, 3). On visiting an older flower the insect will meet the stigma projecting further from the upper lip on the elongated style (Fig. 562, 2) (cf. p. 570, dichogamy). The stigma is then in the position corresponding to the depressed half-anthers, and will receive with certainty the pollen deposited from them on the back of the bee.

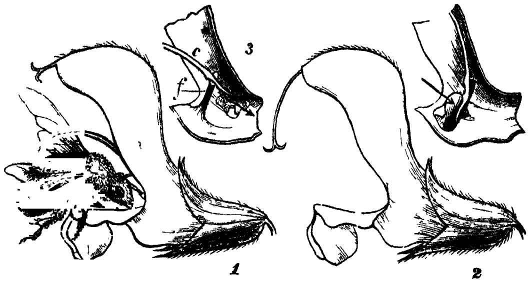


FIG. 562 —Pollination of *Salvia pratensis*. Explanation in the text. (After F. NOLL)

In addition to the stimulus of hunger, plants utilise the reproductive instinct of insects for securing their pollination. In the well-known hollow, pear-shaped inflorescences of the Fig (*Ficus carica*, Fig. 563) there occur, in addition to long-styled female flowers that produce seeds, similar gall-flowers with short styles. In each of the latter a single egg is laid by the Gall-wasp (*Blastophaga*), which, while doing this, pollinates the fertile flowers with pollen carried from the male-inflorescence (the Caprificus). The large white flowers of *Yucca* are exclusively pollinated by the Yucca moth (*Pronuba*). The moth escapes from the pupa in the soil at the time of flowering of *Yucca* and introduces its eggs into the ovary by way of the style; in doing this it carries pollen to the stigma. The larvae of the moth consume a proportion of the ovules in the ovary, but without the agency

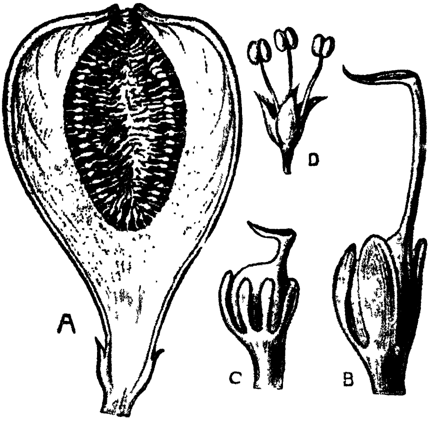


FIG. 563 —*Ficus carica*. *A*, Longitudinal section of an inflorescence *B*, Fertile-flower *C*, Gall flower *D*, Male flower. (*A*–*D*, enlarged, *D*, after KERNER, *B*, *C*, after SOLMS-LAUBACH)

of the moth no seeds will be developed, as is shown by the sterility of the plant in cultivation.

On the continent of America and in the tropics of the Old World, ORNITHOPHILY (9) plays an important part in addition to entomophily; in Europe the conditions for the origin of bird-pollinated flowers appear to be wanting. For according to O. PORSCH it is to the recurring thirst of flower-frequenting birds in hot countries that the appearance of flowers with considerable quantities of nectar of a thin consistency is to be ascribed. A specially remarkable case of adaptation of this kind is afforded by *Strelitzia reginae*, which is often cultivated in green-houses (Fig. 564). Its three outer perianth segments (*t*) are of a bright orange colour; the large azure-blue labellum (*p*) corresponds to one of the inner perianth leaves, while the other two (*p*) remain inconspicuous and roof over the passage leading to the nectary. The stamens (*st*) and the style (*g*) lie in a groove, the margins of which readily separate, formed by the labellum, while the stigma (*g*) projects freely. The similarly-coloured and showy bird (*Nectarinia afra*) flies first to the stigma and touches it, then secures pollen from the stamens, which it will deposit on the stigma of the flower next visited. It is comprehensible from the researches of HESS (p. 565), that many ornithophilous flowers are bright red, also sometimes white, dark purple, blue, green, etc., since the sensitiveness to colours in birds is similar to our own.

Further research is required on the question of the pollination of flowers by bats and snails.

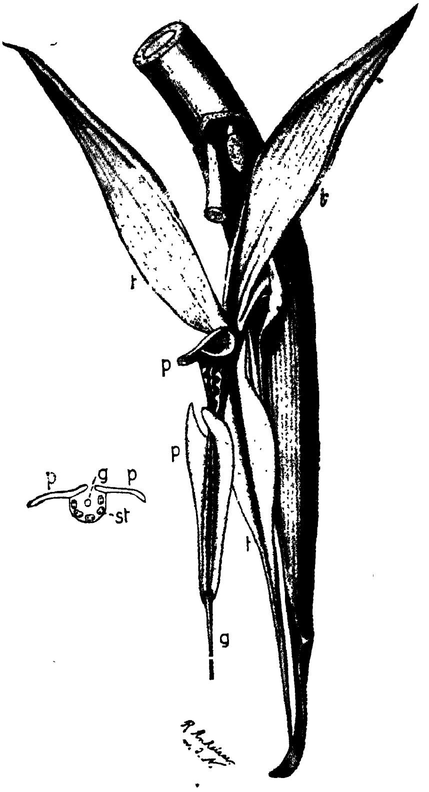


FIG. 564.—Ornithophilous flower of *Strelitzia reginae* and a cross-section of its large labellum (*p*); *t*, outer, and *p*, inner perianth leaves; *g*, style and stigma; *st*, stamens. (From SCHIMPER, *Plant Geography*.)

It would seem remarkable that such manifold and various adaptations for the conveyance of pollen should exist while the majority of angiospermic plants have hermaphrodite flowers; it is known, however, that the pollination of a flower with its own pollen (AUTOGAMY) may result in a poorer yield of seed (Rye) or be without result (self-sterility in *Cardamine pratensis*, *Lobelia fulgens*, *Corydalis cava*, etc.). Cross-pollination (ALLOGAMY) must take place when the pollen can only germinate if the stigma is rubbed, as in the case of *Laburnum vulgare.* The insect visit, which as a rule will bring foreign pollen,

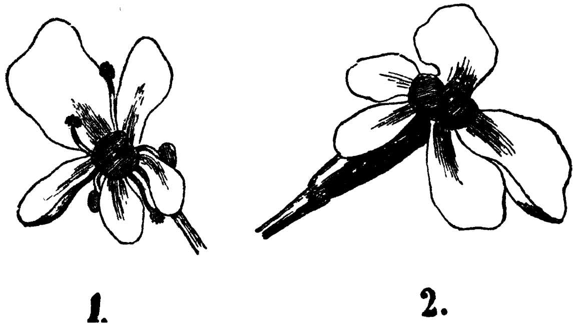


FIG. 565.—Protandrous flower of *Anthriscus sylvestris.* Slightly magnified. *1*, In the male, *2*, in the female condition. (After H. MÜLLER.)

prepares the conditions for germination and excludes the action of the flower's own pollen. In the Orchids the flower's own pollen has a directly injurious influence, and when applied to the stigma causes the flower to wither.

FIG. 566.—Inflorescence of *Plantago media* with protogynous flowers. The upper, still closed flowers (♀) have protruding styles; the lower (♂) have lost their styles, and disclose their elongated stamens. (After F. NOLL.)

Even when there is no self-sterility there are many and various conditions which render the self-fertilisation of hermaphrodite flowers impossible and favour cross-pollination. It is obvious that dioecism completely prevents self-fertilisation, and that monoecism at least hinders the pollination of the flowers with pollen from the same plant. A similar result is brought about when the two kinds of sexual organs of a hermaphrodite flower mature at different times. This very frequent condition is known as DICHOGAMY. There are obviously two possible cases of dichogamy. The stamens may mature first and the pollen be shed before the stigmas of the same flower are receptive; such plants are known as PROTANDROUS. On the other hand, the style with its stigma may ripen first, before the pollen is ready to be shed; the plant is PROTOGYNOUS.

PROTANDRY is the more frequent form of dichogamy. It occurs in the flowers of the Geraniaceae, Campanulaceae, Compositae, Lobeliaceae, Umbelliferae (Fig. 565), Geraniaceae, Malvaceae (Fig. 725), etc. The anthers, in this case, open and discharge their pollen at a time when the stigmas of the same flowers are still imperfectly developed and not ready for pollination. In *Salvia* also (Fig. 562), protandry is the necessary preliminary to the cross-pollination. In the less frequent PROTOGYNY the female sexual organs are ready for fertilisation before the pollen of the same flowers is ripe, and the stigma is usually pollinated and withered before the pollen is shed (*Scrophularia nodosa*, *Aristolochia clematitis*, *Arum maculatum*, *Helleborus*, *Magnolia*, *Plantago*, Fig. 566).

The effect of HETEROSTYLY discovered by DARWIN is similar. According to TISCHLER (^{9a}) this condition can be altered by the conditions of nutrition. A good example is afforded by *Primula sinensis* (Fig 567). Comparison of the flowers on different individuals shows that they differ as regards the position of the stamens and stigma. There are long-styled flowers, the stigma standing at the entrance to the corolla-tube, while the anthers are placed deep down in the tube; and short-styled flowers, the stigma of which stands at the height of the anthers, and the stamens at the height of the stigma of the long-styled flower. An insect will naturally only touch organs of corresponding height with the same part of its body and thus carry pollen between the male and female organs of corresponding height. Thus cross-pollination is ensured. The relative sizes of the pollen grains (*n*) and stigmatic papillae (*p*) agree with this cross-pollination.

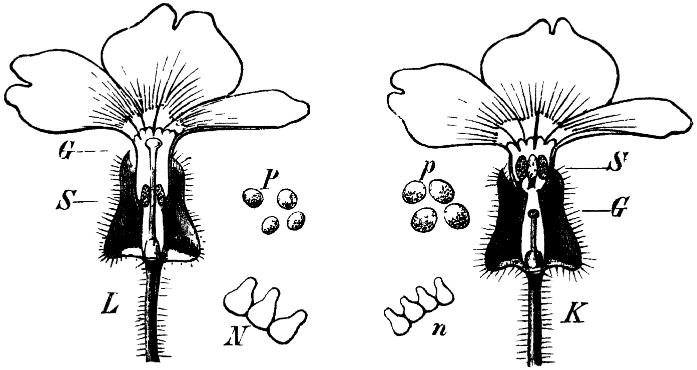


FIG. 567.—*Primula sinensis*: two heterostyled flowers from different plants. *L*, Long-styled, *K*, short-styled flowers; *G*, style; *S*, anthers, *P*, pollen-grains, and *N*, stigmatic papillae of the long-styled form; *p* and *n*, pollen-grains and stigmatic papillae of the short-styled form. (*P*, *N*, *p*, *n*, × 110. After NOLL.)

The same DIMORPHIC HETEROSTYLY is exhibited by *Pulmonaria*, *Hottonia*, *Fagopyrum*, *Linum*, and *Menyanthes*. There are also flowers with TRIMORPHIC HETEROSTYLY (*Lythrum salicaria*, and some species of *Oxalis*), in which there are two circles of stamens and three variations in the height of the stigmas and anthers.

In a great number of flowers self-pollination is made mechanically impossible, as their own pollen is prevented by the respective positions of the sexual organs from coming in contact with the stigma (HERCOGAMY). In the Iris, for example, the anthers are sheltered under the branched petaloid style. The pollinia of *Orchis* are retained in position above the stigma; in *Asclepias* the five pollinia are attached in pairs to swellings of the style by adhesive discs (cf. Fig. 775).

Sometimes hercogamy and dichogamy occur together. The flowers of ***Aristolochia clematitis*** (Fig. 568) are protogynous. The conveyance of pollen from the older to the younger flowers is effected by small insects. The flowers at first stand upright with a widely-opened mouth (Fig. 568 *I*), and in this condition the insects can easily push past the downwardly-directed hairs which clothe the tubular portion of the corolla and reach the dilated portion below. Their exit is, however, prevented by the hairs until the stigma has withered and the anthers have shed their pollen. When this has taken place (Fig. 568 *II*), the hairs dry up, and the insects covered with pollen can make their way out and convey the pollen to the receptive stigmas of younger flowers.

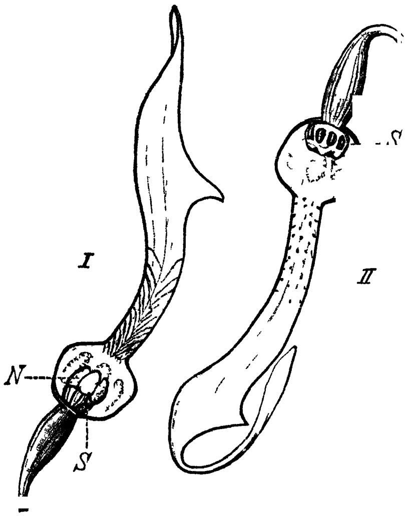


FIG. 568. — Flowers of *Aristolochia clematitis* cut through longitudinally *I*, Young flower in which the stigma (*N*) is receptive and the stamens (*S*) have not yet opened. *II*, Older flower with the stamens opened, the stigma withered, and the hairs on the corolla dried up (× 2 After F. NOLL.)

All these varied and often highly specialised arrangements to ensure crossing indicate a tendency to favour the union of sexual cells which differ in their hereditary characters more widely from one another than would be the case if derived from the same flower. The progeny from allogamous fertilisation tend to be stronger than from autogamous fertilisation.

In certain plants, in addition to the large CHASMOGAMOUS flowers, pollinated by wind or insects, small inconspicuous flowers occur which never open and only serve for self-fertilisation; these CLEISTOGAMOUS flowers (10) afford a further means of propagating the plant, while the plants have the opportunity of occasional cross-pollination owing to the presence of the large chasmogamous flowers. Cleistogamy is of frequent or regular occurrence in species of *Impatiens*, *Viola*, *Lamium*, and *Stellaria*, in *Specularia perfoliata*, *Juncus bufonius*, etc. *Polycarpon tetraphyllum* has only cleistogamous flowers.

Development of the Sexual Generation in the Phanerogams

A. In the **Gymnosperms** a prothallium consisting of a few cells is formed on the germination of the MICROSPORE. This lies within the large cell, which will later give rise to the pollen-tube, closely applied to the cell-wall; the nucleus of this cell is marked *k* in Fig. 569. The first-formed cell (*p*) corresponds to the vegetative cells of the prothallium. The SPERMATOGENOUS CELL (*sp*), which is cut off last, divides later into the generative cell or antheridium (Fig. 570 *B*, *m*), and a STERILE SISTER-CELL (*s*) adjoining the other prothallial cells. It is by the breaking down or the separation of the sterile sister-cell, which is termed a dislocator cell by GOEBEL, that the antheridial cell becomes free to pass into the pollen tube. There, or before its separation, it divides into two daughter-cells; these are the SPERM CELLS or MALE SEXUAL CELLS.

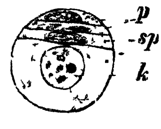


FIG 569 —Pollen grain of *Ginkgo biloba* still within the microsporangium (See text) (×300 After STRASBURGER)

(a) Cycadeae (11)

In the Cycadeae and in *Ginkgo* these male-cells still have the form of spermatozoids, and thus connect directly with the heterosporous Archegoniatae. Their mode of development is shown for *Zamia* in Fig 570. The description of the figure deals with the details. As is further shown in Fig. 571 (*a*) the two spermatozoids remain for a time back to back attached to the sister-cell of the antheridium; after their separation (*b*) they round off, the anterior end being provided with a spirally-arranged crown of cilia by means of which they are capable of independent movement (Fig. 572).

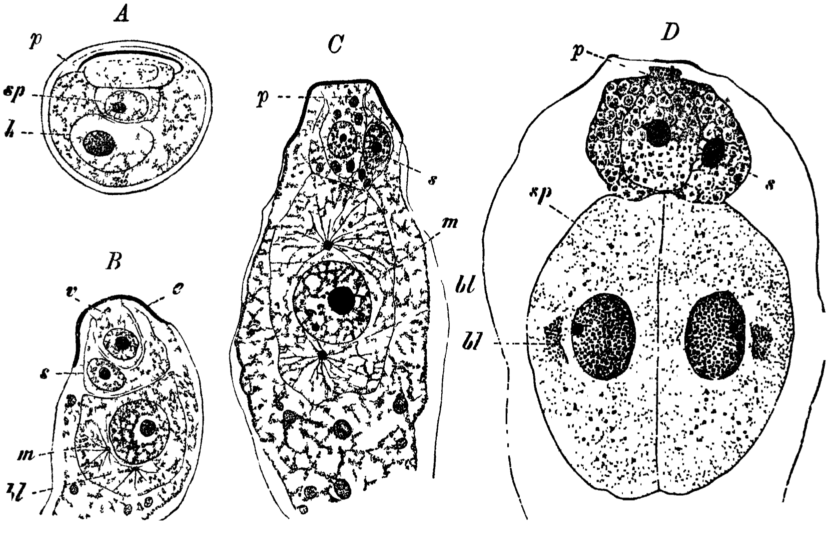


FIG 570 —Formation of spermatozoids in *Zamia floridana* *A*, Mature pollen grain (× 800); *B*, *C*, *D*, Stages in the development of the antheridium (*B*, *C* × 400, *D* × 200), *k*, nucleus of the pollen tube, *sp*, spermatogenous cell, *p*, persisting vegetative prothallial cell growing into the sterile sister cell (*s*) of the antheridium (*m*), *e*, exine, *bl*, blepharoplasts which in *D* are composed of small granules, in the course of forming the cilia Starch grains are present in the pollen tube, and in *C* they are appearing in the vegetative cell and the sister cell, both of which in *D* are packed with starch In *D* the two spermatozoids (*sp*) derived from the antheridium are seen divided from one another by a wall (After H J WEBBER)

The female cones of *Zamia* bear numerous sporophylls, the hexagonal, shield-shaped, terminal expansions of which fit closely together. Each sporophyll bears a pair of macrosporangia. The macrosporangium consists of the nucellus and an integument. The micropyle forms an open canal above the tip of the nucellus. At the period during which the male-cones are shedding their pollen, the macrosporophylls become slightly separated from one another so that the wind-borne pollen-grains can readily enter. A more or less extensive cavity (POLLEN-CHAMBER, Fig. 573) has by this time been formed at the apex of the nucellus, while the disintegrated cells, together perhaps with fluid excreted from the surrounding cells of the nucellus, have given rise to a sticky mass which fills the micropylar canal and forms a drop at its entrance. The pollen-grains reach this drop, and, with the gradual drying up of the fluid, are drawn through the micropylar canal into the pollen-chamber.

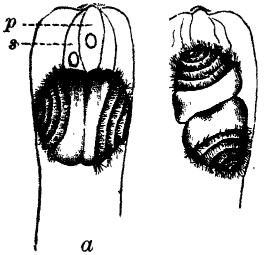


FIG. 571.—Upper end of the pollen-tube of *Zamia floridana*, showing the vegetative prothallial cell (*p*), the sterile sister-cell (*s*), and the two spermatozoids. *a*, Before movement of the spermatozoids has commenced; *b*, after the beginning of ciliary motion; the prothallial cells are broken down and the separation of the two spermatozoids is taking place. (× circa 75. After H. J. WEBBER.)

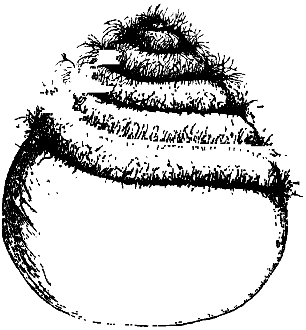


FIG. 572.—*Zamia floridana*. Mature, free-swimming spermatozoid. (× 150. After H. J. WEBBER.)

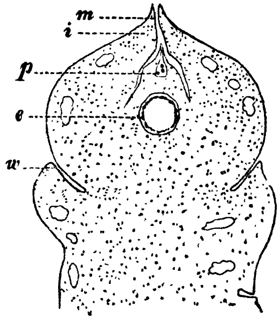


FIG. 573.—Longitudinal section of a young macrosporangium of *Ginkgo biloba*. *m*, Micropyle; *i*, integument; *p*, pollen-chamber; *e*, embryo-sac; *w*, outgrowth of sporophyll. (× 35. After COULTER and CHAMBERLAIN.)

During the development of the pollen-tube and the formation of the motile spermatozoids (Figs. 570, 571), the embryo-sac, filled with the prothallial tissue, is increasing in size within the nucellus.

As in the Coniferae (Fig. 580), the embryo-sac arises by the tetrad

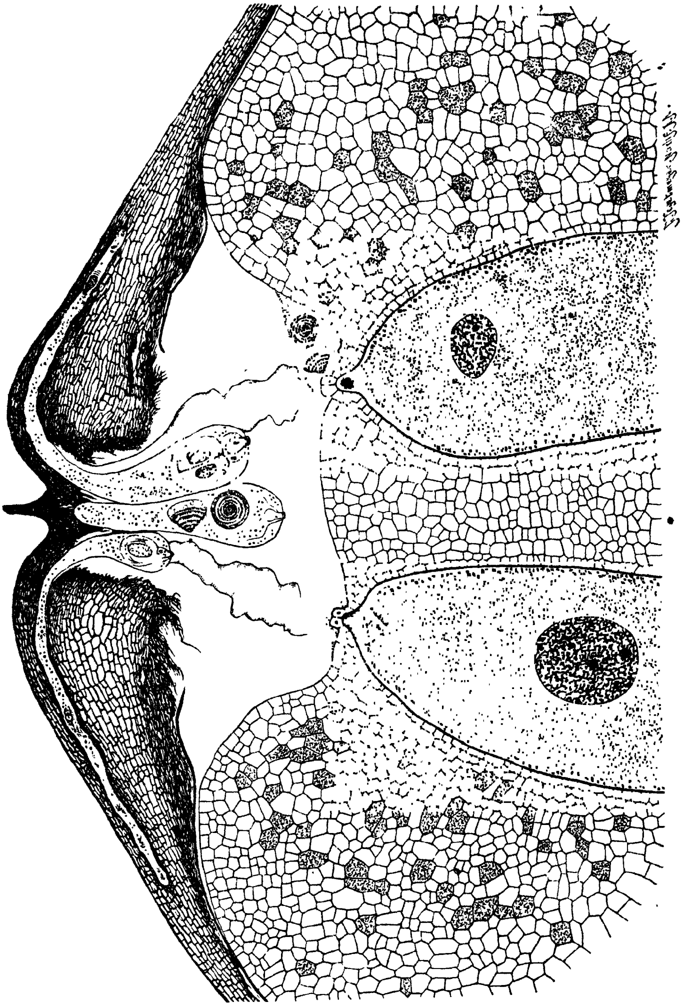


FIG. 574.—*Dioon edule.* Upper portion of the nucellus at the period of fertilisation. The pollen-tubes have grown down from the pollen-chamber through the nucellus after becoming attached by lateral outgrowths. They have reached the archegonial chamber and two of them have already liberated their contents. Two large archegonia with projecting neck-cells are present. (After CHAMBERLAIN.)

division of an embryo-sac mother-cell which usually crushes the other sporogenous cells, as in the case of the macrosporangium of *Selaginella.* Of its four daughter-cells only one persists as the embryo-sac. The tissue of the upper portion of the nucellus disappears and the embryo-sac thus approaches the base of the pollen-chamber. At the apex of the embryo-sac are found the large archegonia, usually four in number, and separated from one another by some layers of cells. Each archegonium has a neck, and ultimately cuts off a ventral canal-cell. The archegonia are situated at the base of a depression in the prothallium, the archegonial chamber (Fig. 574), which in *Dioon* is about 1 mm. in depth and 2 mm. across. The pollen-tubes grow into this depression and, perhaps with the co-operation of the prothallial and dislocator cells, liberate their spermatozoids together with a drop of watery fluid in which they swim. The spermatozoids require to narrow considerably in order to pass through the space between the neck-cells. The spermatozoid strips off the ciliated band on entering the protoplasm of the egg, and its nucleus fuses with that of the latter. The nucleus of the fertilised ovum (Fig. 575) soon divides, and the daughter-nuclei continue to divide rapidly, until after the eighth division there are about 256 free nuclei within the cell. These are crowded towards the lower end of the fertilised egg, where cell-walls commence to form between them.

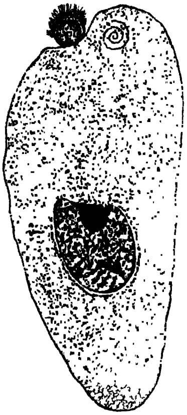


FIG. 575.—*Zamia floridana.* An ovum immediately after the fusion of the nucleus of a spermatozoid with the female nucleus has taken place. The ciliary band of the spermatozoid remains in the upper portion of the protoplasm of the ovum. A second spermatozoid has attempted to enter the ovum. (× 18. After H. J. WEBBER.)

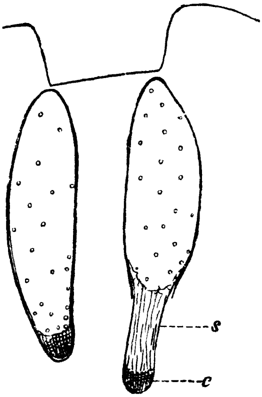


FIG. 576.—Two young pro-embryos of *Dioon edule* showing their relation to the archegonial chamber. *S*, suspensor; *e*, embryo. (After CHAMBERLAIN.)

The so-called PRO-EMBRYO is thus formed (Fig. 576), at the growing end of which the embryo develops from relatively few cells. The cells farther back elongate greatly and as a SUSPENSOR carry the embryo into the prothallus. This in Spermatophytes is termed the ENDOSPERM and serves as a nutritive tissue for the growing embryo. The latter ultimately develops, at the end directed into the prothallus, two large COTYLEDONS between which is the rudiment of the apical bud or PLUMULE The region of the stem below the cotyledons is termed the HYPOCOTYL, it passes gradually into the main root or RADICLE, which is always directed towards the micropyle.

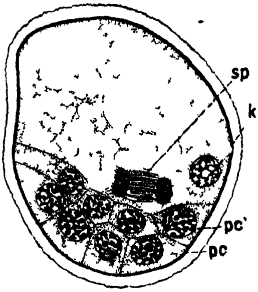


FIG 577 —Pollen grain of *Araucaria brasiliensis* with a multicellular prothallus (*pc* *pc'*) and the antheridium (generative cell, *sp*) in process of division, *k*, nucleus of the pollen-tube (After L BURLINGAME × 616)

(b) Coniferae (12)

The development of the microspores of the Coniferae when they germinate differs from the process described above The prothallial cells, the number of which in the ancient genus *Araucaria* (Fig. 577) is larger than in the other Coniferae and the Cycadeae, soon collapse (Fig 578 *A, B*), and the male cells never have the form of spermatozoids.

The division of the spermatogenous cell produces in *Araucaria* the

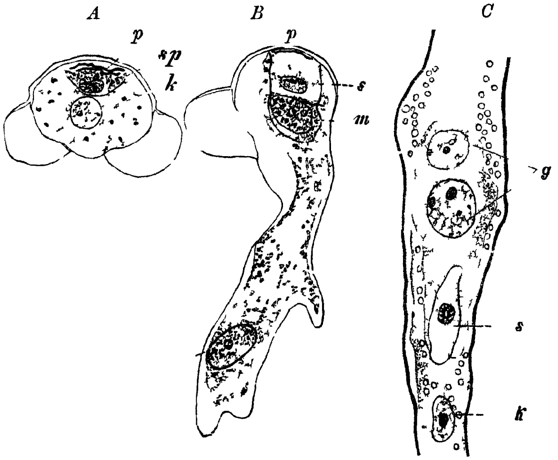


FIG 578 —Development of the pollen tube *A*, *B*, *Pinus laricio* (× 300 After COULTER and CHAMBERLAIN) *C*, *Picea excelsa* (× 250 After MIYAKE) *p*, Remains of the prothallial cells, *sp*, spermatogenous cell, *m* antheridium (generative cell), *s*, its sterile sister cell, *g*, sperm-nuclei of unequal size in a common protoplasmic body, *k*, pollen-tube nucleus

sterile cell (GOEBEL'S dislocator cell) and the antheridial cell which is set free by the breaking down of the former. It gives rise to two sperm-nuclei which are at first of equal size and enclosed in a common protoplasmic mass; it appears, however, that one of them gradually diminishes in size and disappears. This has become the rule in the Taxaceae. As Fig. 579 shows, *Torreya taxifolia*, one of this group from North America, contains in its pollen-tube besides the tube nucleus (*k*) and the sterile sister-cell (*s*), a large functional sperm-nucleus (sp^1), along with an infertile sperm-nucleus (sp^2) less than half its size; each of these has its own protoplasmic investment. The difference in size is still more striking in *Taxus*. While all the Cupressineae have two equal sperm-cells, the Abietineae, like the Araucarieae and Taxaceae, have two unequal sperm-nuclei in a common protoplasmic mass (Fig. 578). Only the larger, which is nearer the tip of the pollen-tube, is fertile.

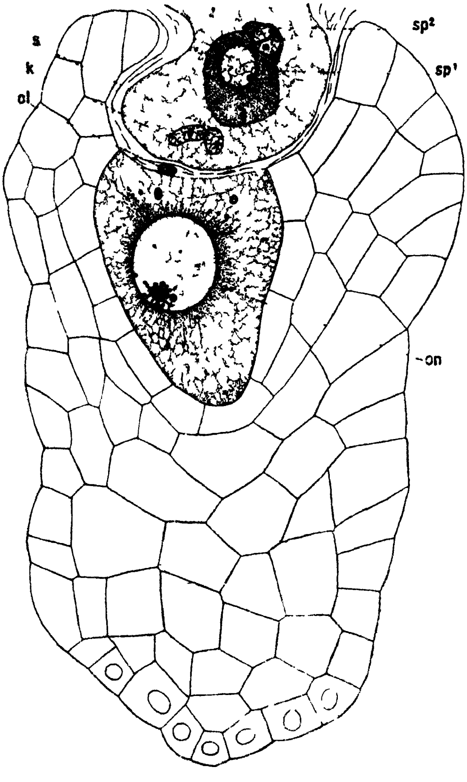


FIG. 579.—*Torreya taxifolia* Longitudinal section of a female prothallus with a large egg-cell and its nucleus (*on*), and the small ventral canal cell (*cl*) The end of a pollen-tube has entered above and contains the nucleus of the pollen tube (*k*) that of the sterile sister-cell (*s*) and two sperm-cells (sp^1, sp^2) of which only the larger (sp^1) is functional (After COULTER and LAND.)

As a rule the macrosporophylls bear two macrosporangia. The single mother-cell undergoes a tetrad division (Fig. 580), and of the four resulting cells only one develops into an embryo sac (macrospore). This, as it increases in size, first crushes its sister-cells and later the whole sporogenous complex of cells. Meanwhile, by the repeated division of the nucleus and protoplasm, the macrospore becomes filled with the tissue of the prothallium (Fig. 581). The archegonia are formed at the apex of the prothallium; each consists of a large ovum and a short neck. As in the Pteridophytes, a small ventral-canal-cell is cut off from the egg-cell shortly before fertilisation (Fig. 582).

The process of fertilisation may be illustrated by *Torreya taxifolia*. The tip of the pollen-tube after breaking down the overlying wall enters the egg-cell and the fertile sperm-nucleus becomes applied to the nucleus of the egg, while the protoplasm of the sperm-cell still surrounds the two nuclei. The rest of the contents of the pollen-tube, as represented in Fig. 579, become compressed in the upper portion of the egg-cell. A later stage of the fusion of the two sexual nuclei is shown for *Picea excelsa* in Fig. 584 *A*.

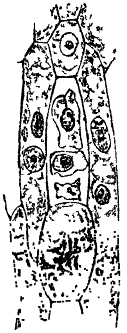


FIG. 580. —*Taxus baccata*. Longitudinal section through the sporogenous tissue, showing an embryo-sac mother-cell which has undergone the tetrad division; three of the facultative macrospores are degenerating, while the fourth is undergoing further development. (× 250. After STRASBURGER.)

In some cases (perhaps indeed in all Cycadeae and Coniferae) the union of the nuclei is far more complicated than has been hitherto assumed to be the case. Thus in *Abies balsamea*, as described by HUTCHINSON, each of the two nuclei after they have joined undergoes a division, in which the haploid number of chromosomes can be recognised. The chromosomes become associated in pairs, this corresponding to the true fusion, and present an appearance similar to that seen in the diakinesis stage of the heterotypic division. By a transverse division of each pair and a separation of the two longitudinal halves, the requisite diploid number is established. According to CHAMBERLAIN the Cycad *Stangeria* follows the same scheme.

The development of the embryo from the fertilised ovum presents differences in the several genera, and the following description applies to the species of *Pinus* (Fig. 584).

By two successive divisions of the nucleus four nuclei are formed which pass to the base of the egg-cell, where they arrange themselves in one plane and undergo a further division (*C*). Cell-walls are formed between the eight nuclei to give rise to an eight-celled pro-embryo. The cells form two tiers, those of the upper tier being in open communication with the cavity of the ovum. The four upper cells then undergo another division (*F*), and this is followed by a similar division of the four lower cells (*G*). The PRO-EMBRYO thus consists of four tiers, each containing four cells, the cells of the upper tier being continuous with the remaining portion of the ovum. In the further development of the three lower tiers, the cells of the upper tier, termed the rosette (Fig. 585 *r*), become separated from the egg-cell by a thickened basal wall (Fig. 585 *p*). The middle tier elongates to form the SUSPENSOR (Fig. 584 *I*, *s*), pushing the terminal tier, from which the embryo will arise, into the tissue of the prothallium or endosperm ; the cells of the latter are filled with nutritive reserve-material.

According to recent investigations by BUCHHOLZ the suspensor-cells bearing the potential embryos always separate from one another in *Pinus* (Fig. 585), so that every fertilised archegonium gives rise to four embryos. Since several archegonia are, as a rule, fertilised, the result is a well-marked polyembryony. The suspensor-cells do not undergo any transverse divisions ; the uppermost cells of the embryos develop as embryonic tubes and contribute to the elongation initiated by the suspensor. The embryo which has thus penetrated furthest into the nutrient prothallial tissue is the successful one in this competition and remains as the single embryo of the seed.

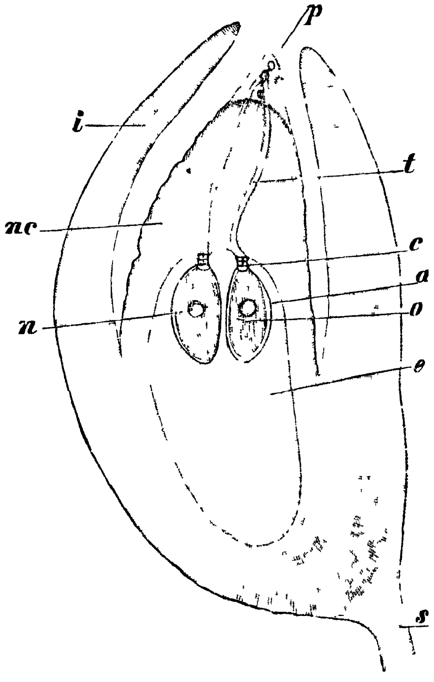


FIG. 581.—Median longitudinal section of an ovule of *Picea excelsa* at the period of fertilisation. *e*, Embryo-sac filled with the prothallium ; *a*, archegonium showing ventral (*a*) and neck portion (*c*) ; *o*, egg-cell ; *n*, nucleus of egg-cell ; *nc*, nucellus ; *p*, pollen-grains ; *t*, pollen-tube ; *i*, integument ; *s*, seed-wing. (× 9 After STRASBURGER.)

The splitting of the embryos takes place at about the same period of development in *Pinus* and *Cedrus*, while it occurs somewhat later in *Tsuga*. In *Abies*, *Picea*, *Larix*, and *Pseudotsuga* no splitting takes place, and a single embryo is produced from each fertilised archegonium. This then has the segmentation already described for the Cycadeae, but the number of cotyledons in the Coniferae, and especially in the Abietineae, is frequently greater than two.

(c) Gnetineae (13, 19a)

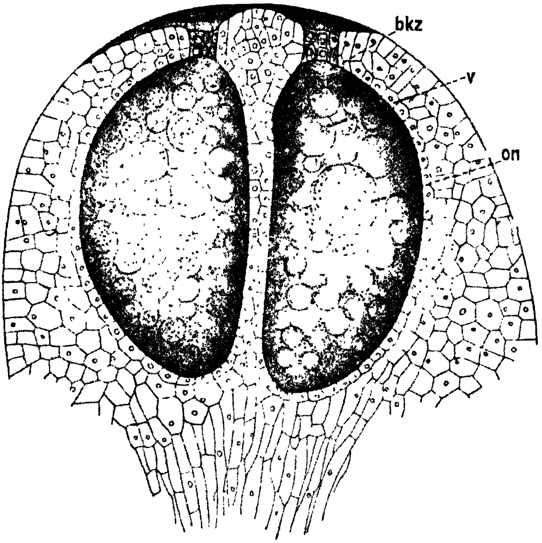


FIG. 582. Longitudinal section of the apical portion of an embryo-sac of *Picea excelsa* showing two archegonia; *bkz*, ventral-canal-cell; *on*, nucleus of egg-cell; *v*, vacuoles containing albuminous material. (× 80 After STRASBURGER.)

The last Order of Gymnosperms, the Gnetineae, exhibit a peculiar and isolated course of development. The microspores in their development and germination show no essential differences from those of other Gymnosperms; the separation of the sperm-cells is, however, less clear and sometimes wanting (as has been shown above for the Cupressineae), in that two similar nuclei lie in a common protoplasmic investment. The macrospores show more marked peculiarities. The macrospores of *Ephedra* and *Welwitschia* have well-developed prothallia. *Ephedra* forms archegonia which on the whole resemble those of the Coniferae. *Welwitschia* has elongated cells with 2-5 nuclei which grow from the summit of the prothallus into the tissue of the nucellus towards the entering pollen-tubes. Their significance as archegonia is rendered more probable by the venter-like basal enlargement. In *Gnetum* (Fig. 586) no prothallium is formed, but the embryo-sac becomes filled with protoplasm in which are numerous nuclei. Each of the two sperm-nuclei from the pollen-tube fuses with a female nucleus, and

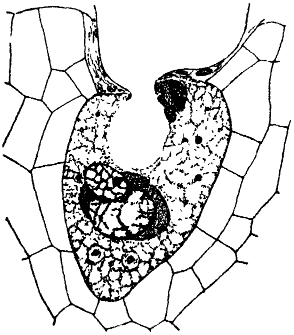


FIG. 583. Fertilisation in *Terreya taxifolia*. (After COULTER and LAND). Description in text.

endosperm-formation then begins. The entrance of both the male nuclei here must be considered in relation with the "double fertilisation" in Angiosperms.

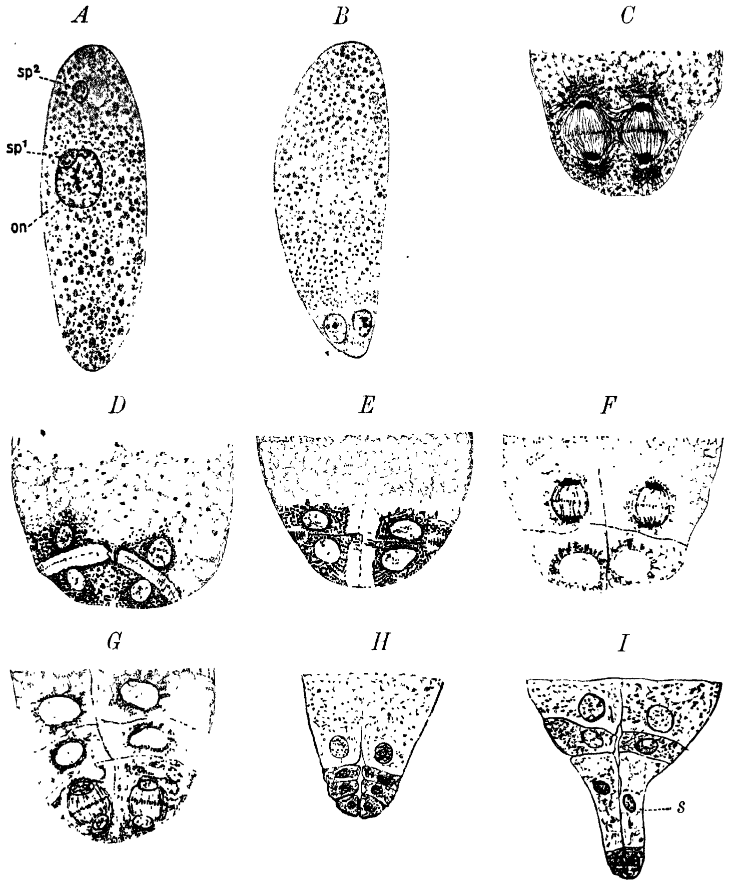


FIG. 584.—*A B*, *Picea excelsa* (× 73, after K. MIYAKE). *C-I*, *Pinus laricio* (*C-G* × circa 200, after N. I. KILDAHL; *H*, *I* × 104, after COULTER and CHAMBERLAIN). Description in the text: *on*, nucleus of ovum; *sp*¹ *sp*², sperm-nuclei; *s*, suspensor.

Of all the young embryos resulting from the penetration of a number of pollen-tubes to the embryo-sac only one continues its development.

B. Angiosperms (14)

(*a*) The MICROSPORES of Angiosperms before they are shed from the pollen-sac form a generative cell (antheridium) (Fig. 587 *A*, *m*) which is clearly delimited from the large pollen-tube cell, but is not enclosed by a cell-wall. It becomes separated from the wall of the pollen-grain, and at the time the pollen is shed appears as a spindle-shaped structure in the centre of the microspore beside the vegetative nucleus (*k*). When the pollen-grain germinates on the stigma it passes into the pollen-tube, and its nucleus sooner or later divides into two sperm-nuclei (*g*) which lie free in the protoplasm within the pollen-tube without being enclosed in a common mass of protoplasm. They are of an elongated oval or ellipsoidal shape and pass one after another down the pollen-tube. The nucleus of the pollen-tube (*k*) is usually visible in the neighbourhood of the sperm-nuclei. The absence of the small prothallial cells, and of a sterile sister-cell of the antheridium, as well as the absence of a cell-wall from the antheridium, and lastly the presence of naked sperm-nuclei instead of sperm-cells in the pollen-tube, are points in which the Angiosperms differ from Gymnosperms. The appearance of two sperm-cells, which was first observed by HERRIG in artificial germinations of pollen-grains of Monocotyledons, has since been shown by WYLLIE to occur on normal germination of the pollen of *Vallisneria spiralis*, and by FINN to occur in *Asclepias cornuti* and two species of *Vincetoxicum*. It is thus more

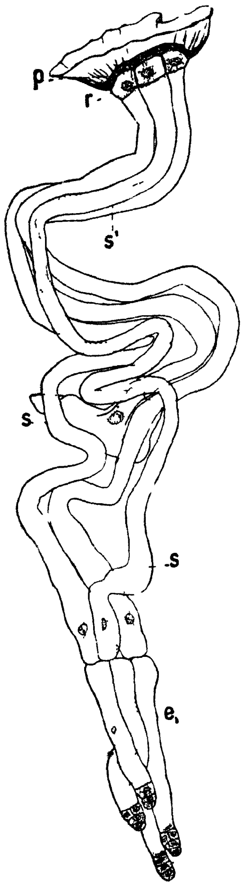


FIG. 585.—Further developed embryo of *Pinus Banksiana*. *s*, Suspensor; *e*, primary embryonic tubes, *r*, rosette, *p*, basal wall (× 80, after J. T. BUCHHOLZ)

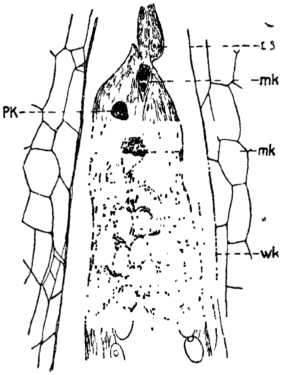


FIG 586.—Apex of the embryo sac of *Gnetum Rumphianum* shortly before the development of the female-cells. *wk*, Female-nuclei; *mk*, male-nuclei; *PK*, pollen-tube-nucleus; *ps*, pollen-tube.

wide-spread both among Monocotyledons and Dicotyledons than had been thought. The fact that according to RUHLAND and WETZEL chloroplasts are present in the sperm-cells has important bearings on some genetic problems

(*b*) MACROSPORES (1) —The characteristic differences which the Angiosperms show from the general course of development of the MACROSPORANGIUM in the Gymnosperms commence with the cell-divisions in the single, functional, macrospore-mother cell resulting from the tetrad division (Fig. 588, 1-5). The "PRIMARY NUCLEUS of the embryo sac" divides and the daughter nuclei separate from one another. They divide twice in succession, so that eight nuclei are present After this, cell-formation commences around these nuclei (Fig 588, 6-8). Both at the upper or micropylar end of the embryo-sac and at the lower end three naked cells are thus formed. The two

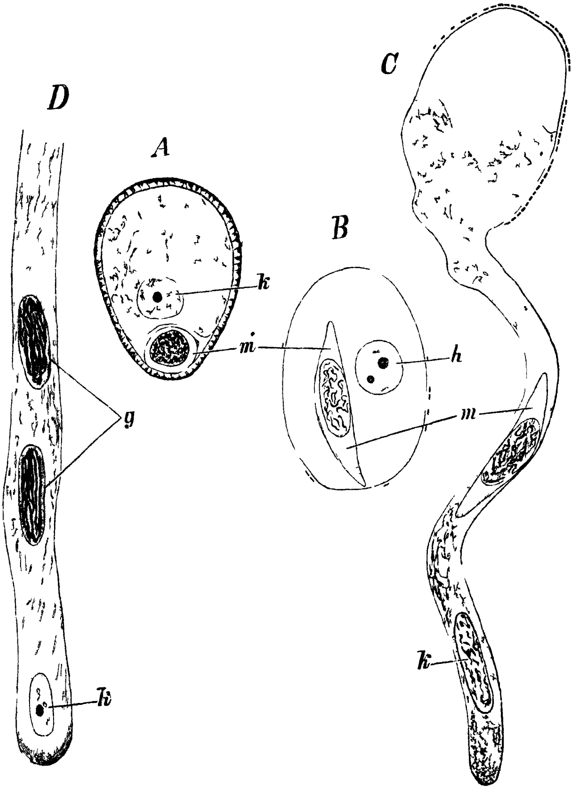


FIG 587 —Pollen grain of *Lilium Martagon* and its germination *k*, Vegetative nucleus of the pollen grain, *m*, antheridium, *g*, sperm nuclei (× 400 After STRASBURGER)

remaining "POLAR NUCLEI" move towards one another in the middle of the embryo-sac, and fuse to form the "SECONDARY NUCLEUS of the embryo-sac." The three cells at the lower end are called the ANTIPODAL CELLS; they correspond to the vegetative prothallial cells, which in the Gymnosperms, including *Gnetum*, fill the cavity of the macrospore.

The three cells at the micropylar end constitute the "EGG APPARATUS" (Fig. 590). Two of them are similar and are termed the SYNERGIDAE, while the third, which projects farther into the cavity, is the EGG-CELL or OVUM itself. The synergidae assist in the passage of the contents of the pollen-tube into the embryo-sac. Here also the process of reduction has gone as far as possible; in place of the more or less numerous archegonia of the gymnospermous macrospore only a single egg-cell is present. The synergidae may either be regarded as archegonia which have become sterile or, with TREUB and PORSCH, as neck-cells of an archegonium transformed to the egg-apparatus (Fig. 590).

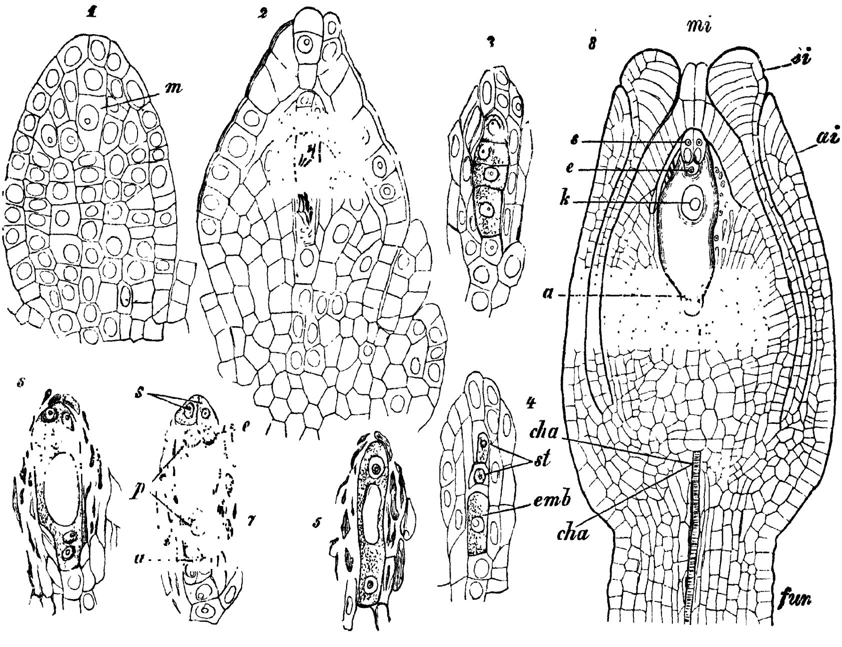


FIG. 588.—Development of the embryo-sac in *Polygonum divaricatum.* *m*, Mother-cell of the embryo-sac; *emb*, embryo-sac; *st*, sterile sister-cells; *e*, egg-cell; *s*, synergidae; *p*, polar nuclei; *a*, antipodal cells; *k*, secondary nucleus of the embryo-sac; *cha*, chalaza; *mi*, micropyle; *ai*, *ii*, outer and inner integuments; *fun*, funiculus. (*1-7*, × 320; *8*, × 135. After STRASBURGER.)

The type of embryo-sac development described above may be regarded as normal for the Angiosperms (15a) and be termed with GOEBEL the eight-nucleus type. Many plants, however, exhibit other developments of their macrospores. These have been summarised and discussed by RUTGERS.

GOEBEL regards the various other types of development and the resulting types of embryo-sac as variants of the eight-nucleus type. In *Lilium* the division of the macrospore-mother-cell is omitted, so that it becomes converted directly into the embryo-sac, in which the reduction-division takes place; this is termed by GOEBEL a coeno-macrospore, corresponding to the four possible macrospores. Eight nuclei may be formed in this embryo-sac (*Lilium*), or the process may go further and there may be sixteen nuclei as in *Peperomia*, the Penaeaceae, *Euphorbia procera*, etc. Variants leading to a diminution in the number of nuclei are more common. Thus *Pedilanthus* has five nuclei; four nuclei are present in the embryo-sacs of *Oenothera* and *Codiaeum* after a normal tetrad division of the mother-cell, in *Cypripedium* after a single division, and in *Helosis* without precedent division of the mother-cell. These four nuclei may give rise to the ovum, one synergida and polar nuclei; or, as in the embryo-sac of *Plumbagella*, which arises without division of the mother-cell, to the egg-cell, polar nuclei, and one antipodal cell. As a rule the micropylar end of the embryo-sac, as the more important, shows less reduction than the chalazal end. No explanation can be suggested for the reduced development in these cases. In the Podostemaceae, which, so far as an embryo-sac can be recognised in them, have the four-nucleus type, this may perhaps be explained by their peculiar conditions of life; these plants grow in rapidly flowing streams of tropical mountains, and only a short, dry period is available for pollination and the development of the fruit. It appears impossible to draw any conclusions as to the systematic position of

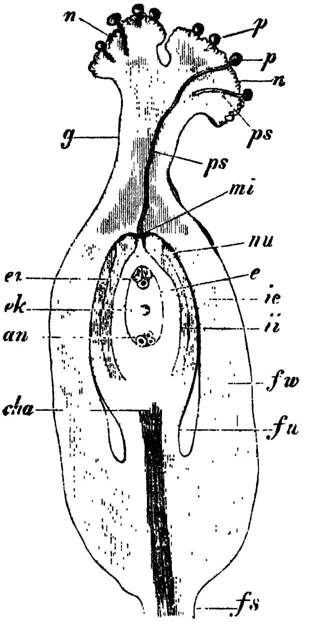


FIG. 589.—Ovary of *Polygonum Convolvulus* with an atropous ovule. (Diagrammatic.) *fs*, Stalk-like base of ovary; *fu*, funiculus; *cha*, chalaza; *nu*, nucellus; *mi*, micropyle; *ii*, inner, *ie*, outer integument; *e*, embryo-sac; *ek*, nucleus of embryo-sac; *ei*, egg apparatus; *an*, antipodal cells; *g*, style; *n*, stigma; *p*, pollen-grains; *ps*, pollen-tube. (× 48. After SCHENCK.)

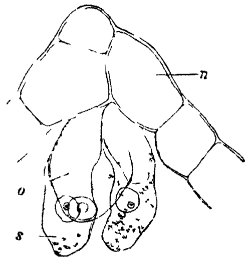


FIG. 590.—*Funkia ovata* Apex of nucellus, showing part of embryo-sac and egg-apparatus before fertilisation, *o*, egg-cell; *s*, synergidae. (× 390. After STRASBURGER.)

plants from the type of construction of their embryo-sacs (see further Schnarf[15a]).

The microspores, which cannot reach the macrospore directly, germinate on the stigma (Fig. 589). The pollen-tube penetrates for the length of the style, and as a rule the tip enters the micropyle of an ovule and so reaches the apex of the nucellus. This most usual course of the pollen-tube is termed POROGAMY, but many cases of departure from it have become known of recent years.

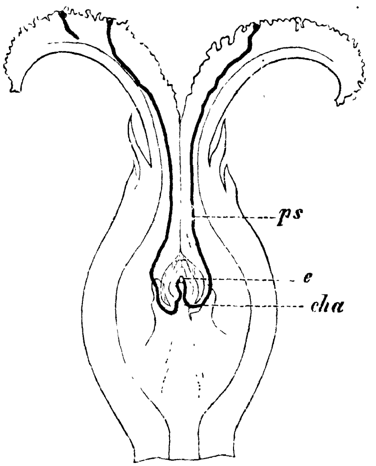


Fig. 591.—Longitudinal section of an ovary of *Juglans regia* to show the chalazogamy. *ps*, Pollen-tube; *e*, embryo-sac; *cha*, chalaza. (Somewhat diagrammatic. × 6.)

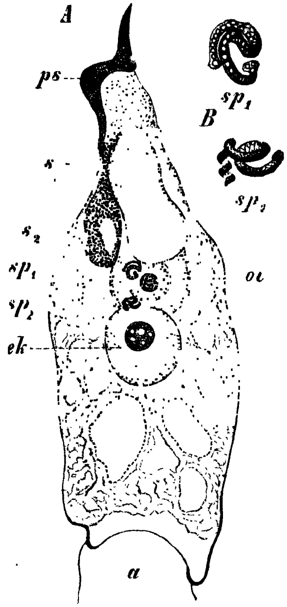


Fig. 592.—*A*, Embryo-sac of *Helianthus annuus* (after Nawaschin). *B*, The male nuclei more highly magnified. *ps*, Pollen-tube; s_1, s_2, synergidae; sp_1, sp_2, male nuclei; *ov*, egg-cell; *ek*, nucleus of embryo-sac; *a*, antipodal cells.

Treub (15) first showed in *Casuarina* that the pollen-tube entered the ovule by way of the chalaza, and thus reached the peculiar sporogenous tissue, which in this case develops a number of macrospores, or embryo-sacs. Chalazogamy, as this mode of fertilisation is termed in contrast to porogamy, has since been shown to occur in a large number of forms. These belong to the Casuarinaceae, Juglandaceae, Betulaceae, Ulmaceae, Celtoideae, Urticaceae, Cannabinaceae, and Euphorbiaceae, which all have the common character of the pollen-tube growing within the tissues, and avoiding entrance by the micropyle. This in some cases (Urticaceae) becomes closed or, as in the Euphorbiaceae, is covered by the obturator. The pollen-tube makes its way to the embryo-sac sometimes from the chalazal end (Fig 591) and sometimes from the side of the ovule, penetrating the tissues that lie between it and the egg apparatus. Since, according to the opinion of many authors, the families mentioned above stand at the lower end of the series of Dicotyledons where a connection with the Gymnosperms might be looked for, this type of fertilisation may be regarded as departing from the behaviour of the more numerous porogamic Angiosperms and approximating to the original relations in Gymnosperms. In the latter the whole overlying tissue of the nucellus has to be penetrated by the pollen-tube to reach the embryo-sac (Fig. 581, cf. also p. 619). NAWASCHIN further shows that there are also indications in the development of the contents of the pollen-tube that these forms are at a lower stage than the majority of Angiosperms. In *Juglans* the two male nuclei remain enclosed by a common protoplasmic mass which even enters the embryo-sac; it then gradually disappears and the naked nuclei emerge and fulfil their respective functions. Probably, however, the above named families are reduced rather than constituting, as these investigators assume, an ascending series. The phenomena are consistent with both views.

When the pollen-tube, containing the two sperm-nuclei, has reached the embryo-sac, its contents escape and pass by way of one of the synergidae to the ovum; this synergida dies. One of the two male nuclei fuses with the nucleus of the ovum, which then becomes surrounded by a cellulose wall. The second male nucleus passes the ovum and unites with the large secondary nucleus of the embryo-sac to form the definitive nucleus of the embryo-sac or the ENDOSPERM NUCLEUS (Fig. 592). Both the male nuclei are often spirally curved like a corkscrew, and NAWASCHIN, who first demonstrated the behaviour of the second male nucleus, compares them to the spermatozoids of the Pteridophyta. The further development usually commences by the division of the endosperm nucleus ([16]). If each nuclear division is followed by a cell-wall the process may be termed a cellular endosperm-formation: this is found in many Compositae, Solanaceae, Primulaceae, *Aponogeton*, *Potamogeton*, etc. (Fig. 593). If on the other hand a large number of nuclei lying in the layer of protoplasm lining the walls are first formed, and then cell-walls are simultaneously produced, the endosperm-formation may be termed nuclear (Fig. 594). Only when the endosperm has developed does the further formation of the embryo in the way first described by HANSTEIN take place (Figs. 595, 596).

The distinctive feature of the development of the endosperm in Angiosperms from the prothallus of Gymnosperms lies in the interruption which occurs in the process in the case of the endosperm. In the embryo-sac, when ready for fertilisation, only an indication of the prothallus exists in the vegetative, antipodal cells. The true formation of the endosperm is dependent on the further development of the embryo-sac, and waste of material is thus guarded against. The starting-point of this endosperm-formation is given by the secondary nucleus of the embryo-sac, which needs to be stimulated by fusion with the second male nucleus to form the endosperm nucleus, before it enters on active division (cf. Gnetaceae).

From the fertilised ovum, enclosed within its cell-wall, a PRO-EMBRYO consisting of a row of cells is first developed; the end cell of this row gives rise to the greater part of the EMBRYO. The rest of the pro-embryo forms the SUSPENSOR. Between the embryo and suspensor is a cell known as the HYPOPHYSIS (Fig. 595), which takes a small part in the formation of the lower end of the embryo. The segmentation of the embryo presents differences according to whether the plant belongs to the Monocotyledons or Dicotyledons. IN THE LATTER, TWO COTYLEDONS ARE FORMED AT THE END OF THE GROWING EMBRYO (Fig. 595 *D*), AND THE GROWING POINT OF THE SHOOT ORIGINATES AT THE BASE OF THE DEPRESSION BETWEEN THEM. MONOCOTYLEDONS, ON THE OTHER HAND, HAVE A SINGLE LARGE TERMINAL COTYLEDON, THE GROWING POINT BEING SITUATED LATERALLY (Fig. 596). In both cases the root is formed from the end of the embryo which is directed towards the micropyle; its limits can be readily traced in older embryos.

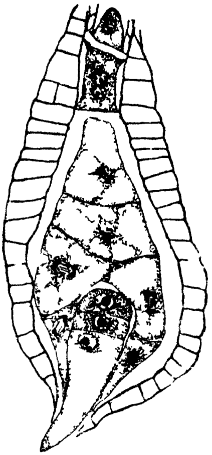


FIG. 593.—Cellular formation of the endosperm in *Ageratum mexicanum*. (After O. DAHLGREN.)

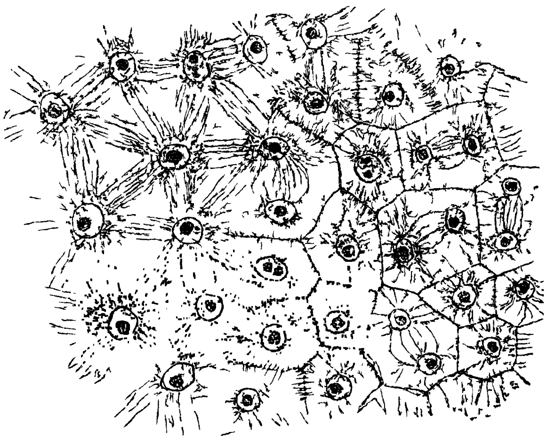


FIG. 594.—Nuclear formation of the endosperm of *Reseda odorata*. (After E. STRASBURGER.)

After fertilisation a considerable accumulation of reserve materials is necessary in the embryo sac both for the development of the embryo and for its future use. It is thus of importance that a means of transfer of these materials should exist. In the simplest cases the endosperm simply enlarges, crushing the surrounding tissues of the nucellus; often the antipodal cells, which are the structures which lie nearest to the chalaza, are entrusted with the function of nourishing the embryo sac. They then increase in number and sometimes undergo considerable further development. Other portions of the embryo sac (16a) may grow out as long haustoria which sometimes emerge from the micropyle and sometimes penetrate the tissue beneath the chalaza. In some cases, especially in insectivorous and semi-parasitic plants, a special store of reserve-material is laid up in this position for transference to the macrospore (Fig. 597).

In some cases plants have more or less completely lost the capacity for sexual reproduction, which has been replaced by other modes of reproduction that can often be distinguished only by careful investigation. Thus in some plants, *e.g. Alchemilla, Thalictrum, Taraxacum*, some Urticaceae, etc., no reduction-division takes place in the development of the embryo-sac. The "egg-cells" are thus not capable of being fertilised; they are not normal sexual cells but possess the character of vegetative cells. Such diploid "egg-cells" are able to develop without a precedent nuclear fusion, and in connection with this (or as its cause?) the pollen is usually sterile. In order to maintain agreement with zoological terminology, this phenomenon, *i.e.* the further development of an egg-cell without fertilisation, may be termed PARTHENOGENESIS.

Since in the above cases the egg-cell was diploid, the phenomenon, may be spoken of as "somatic parthenogenesis." Generative parthenogenesis, *i.e.* the further development of true haploid egg-cells without fertilisation, is not known among Spermatophyta.

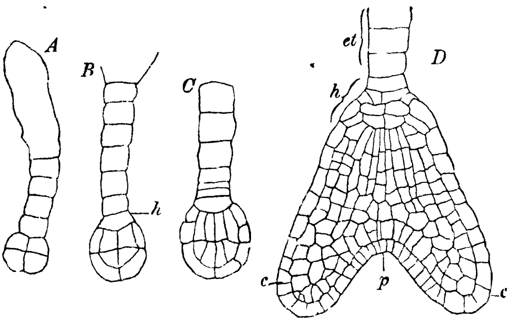


FIG. 595.—Stages in the development of the embryo of *Capsella bursa pastoris* (*A-D*). *h*, Hypophysis; *et*, suspensor; *c*, cotyledons, *p*, plumule. (After HANSTEIN, magnified.)

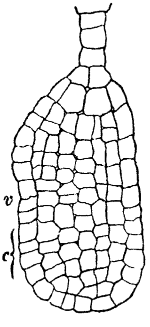


FIG. 596.—Young embryo of *Alisma Plantago*. *c*, Cotyledon; *v*, growing point. (After HANSTEIN, magnified.)

APOGAMY is to be distinguished from parthenogenesis. The development of haploid cells of the embryo-sac, such as the synergidae or the antipodal cells, to produce an embryo would be termed "generative apogamy." The development of embryos from diploid cells of the nucellus, as in *Funkia* (Fig. 598), *Citrus aurantium*, etc., or the experimentally induced adventitious embryos of HABERLANDT (17a) would be "somatic apogamy." Possibly in this case the term "nucellar embryony" would be preferable.

Lastly, by "APOSPORY" is to be understood the origin of gametophytes from tissue of the sporophyte without the presence of spores. Such a case of apospory is clearly shown in Fig. 599. A large vegetative cell, outside the nucellus, though close to it, crushes the macrospore-mother-cell which has already divided into four and enlarges greatly, behaving like an embryo-sac. This "egg-cell" is naturally diploid and forms an embryo without being fertilised.

According to the investigations of **OSTENFELD** and **ROSENBERG**, the genus *Hieracium* is of special interest, since the formation of the embryo within the

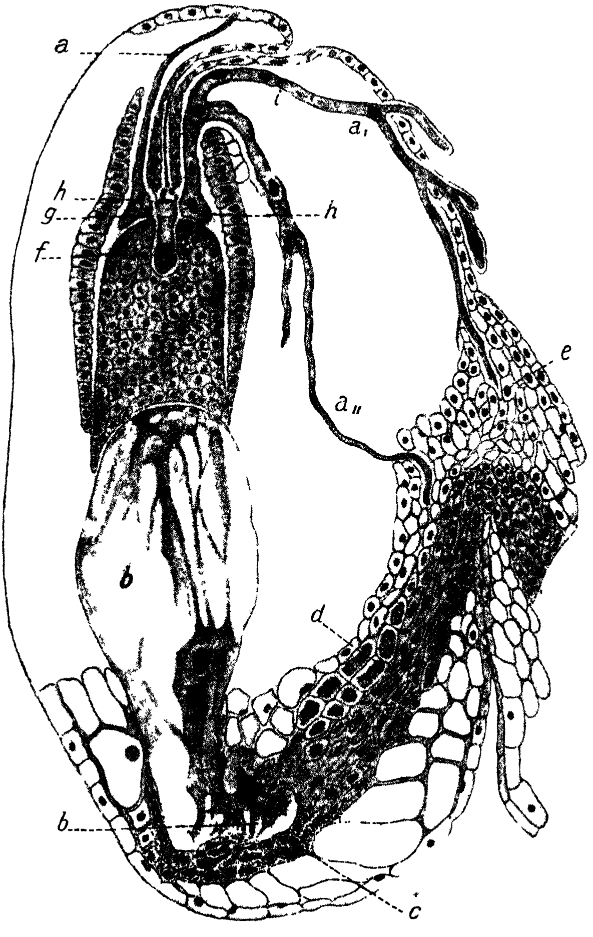


FIG. 597.—Haustoria of the embryo-sac of *Melampyrum nemorosum* (after **BALICKA-IWANOWSKA**). *b*, Haustoria of the chalazal end; *c*, nutritive tissue; *d*, branch of the vascular bundle; *e*, funicle; *f*, embryo; *g*, the suspensor; *a*, $a_{,}$, $a_{,,}$ haustorial tubes arising early from the micropylar end, spreading widely in the funicle and sometimes penetrating the epidermis; *h*, the base of attachment of these; *i*, cross-walls in the tubes.

ovule may commence in very various ways. In most cases a tetrad formation accompanied by a reduction-division takes place, but only some of these ovules are found to have a normal embryo-sac capable of fertilisation; as a rule this is displaced by a vegetative cell which develops into an embryo-sac aposporously (Fig. 599). In exceptional cases embryo-sacs with parthenogenetic egg-cells are formed.

The Seed (16)

The entire structure developed from the ovule after fertilisation is termed the SEED. Every seed consists of the more or less advanced EMBRYO developed from the fertilised ovum, the ENDOSPERM surrounding the embryo, and the protective SEED-COAT. The seed-coat is always derived from the integument or integuments; their cells, by the thickening, suberisation, and lignification of the walls, give rise to an effective organ of protection against drying and injury for the dormant young plant within. A special development of the epidermis of the seed into mucilage-cells is of frequent occurrence (Quince, *Linum*, many Cruciferae, etc.). The mucilage serves as a first means of fixation in the soil and also retains water which is necessary for germination. Such other features of the surface as hairs, prickles, etc., have usually the former function, if they do not stand in relation to the distribution of the seed.

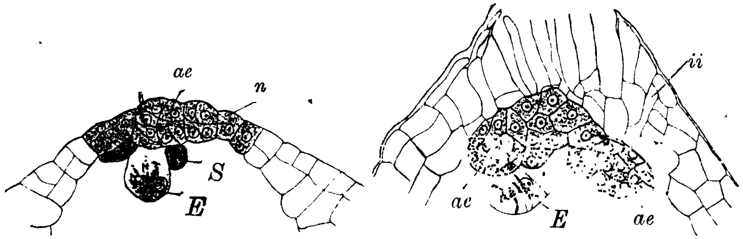


FIG. 598.—Vegetative formation of embryos in *Funkia ovata*. *n*, Nucellus with cells in process of forming the rudiments (*ae*) of the adventitious embryos; *S*, synergidae; *E*, egg-cells, in the figure on the right developing into an embryo; *ii*, inner integument. (After STRASBURGER.)

Points of morphological importance in the seed-coat are (1) the MICROPYLE, (2) the HILUM (=place of attachment to the funicle), and (3) the RAPHE. From what was said above (p. 547) it follows that the micropyle and hilum will lie at opposite poles of the seed when the ovule is atropous. In seeds derived from anatropous ovules (*i.e.* those in which the funicle lies along one side of the ovule, which is bent round at the chalaza) the hilum and micropyle are close together. Only seeds of this kind possess a raphe connecting the hilum and chalazal region. Campylotropous ovules develop into seeds resembling those derived from anatropous ovules, but the embryo is curved.

In some cases the function of the seed-coat is modified owing to the protection of the seed or seeds being undertaken by the pericarp; this or its innermost layers are developed as sclerotic cells and form the stone of the drupe or shell of the nut (cf. p. 595 ff.). In such cases (*e.g.* Almond, Cherry-Laurel, Cherry, Pepper, etc.), since any special development of the seed-coat is unnecessary, it tends to become reduced; its cells do not thicken or modify their walls and the various layers become simply compressed.

The nutritive tissue in the seeds is developed, in the case of Gymnosperms (except in *Gnetum*), by the time of fertilisation and constitutes the prothallium (cf. p. 574 ff.). This fills the embryo-sac and nourishes the embryo, which grows down into it. The surrounding tissue of the nucellus becomes crushed so that the embryo-sac extends to the seed-coat. The cells of the endosperm are packed with reserve-materials (starch, fat, proteid), and these are utilised in the further development of the embryo; this takes place on germination, usually after a period of rest.

The nutritive tissue in the Angiosperms (and of *Gnetum*) arises, on the other hand, after the egg-cell has been fertilised. It originates from the secondary nucleus of the embryo-sac derived by the fusion of the two polar nuclei. This is stimulated to division after fusion with the second male nucleus. (On the two types of endosperm cf. p. 588.)

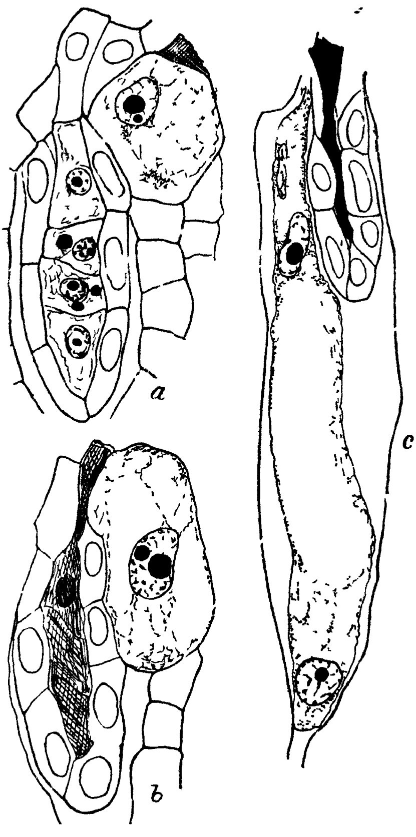


Fig. 599.—Aposporous origin of the embryo-sac of *Hieracium flagellare*. *a*, Normal tetrad of macrospores; *b*, *c*, the disorganisation of this. The diploid embryo-sac arises from a cell of the integument that is recognisable in *a*. (After O Rosenberg and A. Ernst.)

In Angiosperms also the endosperm as a rule compresses the remains of the nucellus. Reserve materials such as starch, fatty oil, and aleurone grains are accumulated in the cells (Fig. 600); in other cases the greatly thickened walls form a store of reserve-cellulose (Fig. 601). In a few cases, as in Piperaceae, Scitamineae, etc., the nucellus persists and also serves as a nutritive tissue; it is then termed PERISPERM (Fig. 602 *B*). When lamellae of the perisperm or of this and the seed coat grow into the endosperm, they usually differ from the latter in colour and contents; the endosperm is then said to be ruminated [*Myristica* (Fig. 639), *Areca*].

In very many cases, *e g.* Leguminosae, Cruciferae, etc., not only is the nucellus absorbed by the endosperm, but the latter is completely displaced by the embryo. The reserve-materials are then stored up in the cotyledons or in the whole body of the embryo (Fig. 603).

Lastly, a structure known as the ARILLUS must be mentioned, which usually stands in relation to the distribution of the seeds. It arises as a succulent (*Taxus*) or dry [*Pahudia javanica* (Leguminosae) *Strelitzia reginae*], and usually brightly coloured outgrowth from the funicle. It grows up around the ovule and ultimately comes to invest the seed more or less completely (Figs. 604 *D*, 605). An outgrowth in the neighbourhood of the micropyle, which is found in the Euphorbiaceae, is termed a CARUNCULA (Fig. 604 *B*, *C*).

The Fruit (16)

The effect of fertilisation is not only seen in the macrosporangia but extends to the macrosporophylls or carpels. The structures of very various form which are formed from the carpels (often together with the persistent calyx and the floral axis) are called FRUITS, and serve primarily to protect the developing seeds. In Gymnosperms, where the ovules are borne freely exposed on the carpels, no fruits in the strict sense can exist, since no ovary is present. Thus in *Cycas*, *Ginkgo*, *Taxus*, *Podocarpus*, *Gnetum*, and *Ephedra* we can only speak of seeds and not of fruits. When, however, the carpels after fertilisation close together, as in the cones of some Gymnosperms and the berry-like cones of *Juniperus*, a structure analogous to the angiospermic fruit is formed, and the term fruit may be used

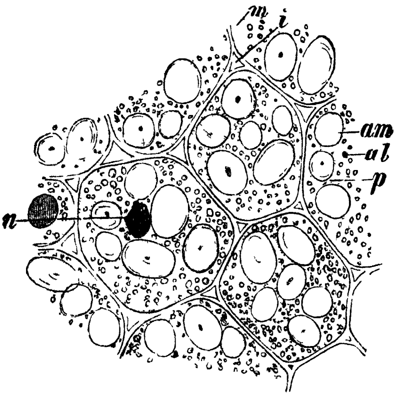


FIG 600 —Part of section through one of the cotyledons of the Pea, showing cells with reserve material. *am*, Starch-grains, *al*, aleurone grains, *p*, protoplasm, *n*, nucleus (× 160 After STRASBURGER)

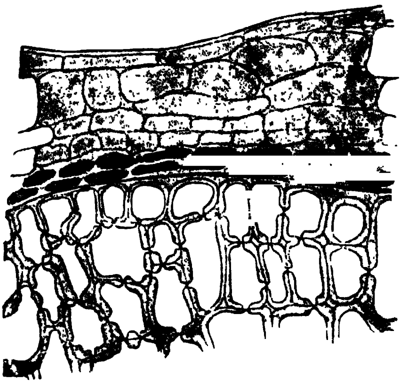


FIG 601 —Transverse section of the seed of *Colchicum*, showing the reserve-cellulose of the endosperm within the seed coat

A great variety in the development of the fruit in Angiosperms might be anticipated from the range in structure of the gynaeceum. The simplest definition of a fruit is the ripened ovary, but difficulties arise in the case of apocarpous gynaecea.

The product of the individual carpels associated in such apocarpous gynaecea as those of the Rosaceae will here be termed PARTIAL FRUITS or FRUITLETS, while the product of the whole gynaeceum will be spoken of as the FRUIT or the COLLECTIVE FRUIT. The hollowed-out or projecting floral axis bearing the carpels may be included in the fruit. Thus the Strawberry is a collective fruit composed of the succulent receptacle bearing the small yellow nut-like fruitlets. In the Apple the core only is the fruit, the succulent tissue being derived from the hollowed floral axis surrounding and fused with the carpels. In the *Rose* there is similarly a collective fruit, the fruitlets being the hard nutlets enclosed by the succulent receptacle (Fig. 606). In the case of fruits resulting from syncarpous gynaecea the further development of the wall of the ovary as the PERICARP has to be especially considered. The outermost, middle and innermost layers of this are distinguished as EXOCARP, MESOCARP, and ENDOCARP respectively.

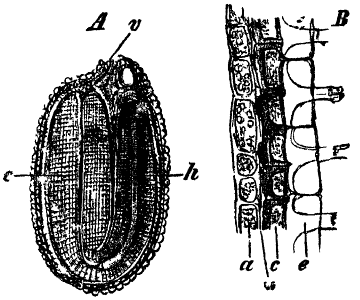


FIG. 603.—*Capsella bursa pastoris* A, Longitudinal section of a ripe seed, *h*, hypocotyl; *c*, cotyledons; *v*, vascular bundle of the funicle (× 26). B, Longitudinal section of the seed-coat after treatment with water; *e*, the swollen epidermis, *c*, brown, strongly thickened layer; *, compressed layer of cells; *a*, the single persisting layer of endosperm cells containing aleurone grains. (× 250. After STRASBURGER.)

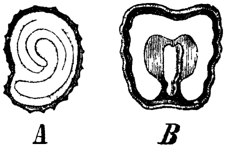


FIG. 602 —*A*, Seed of *Hyoscyamus niger*, showing the dicotyledonous embryo embedded in the endosperm, *B*, seed of *Elettaria Cardamomum*, with perisperm. (After BERG and SCHMIDT.)

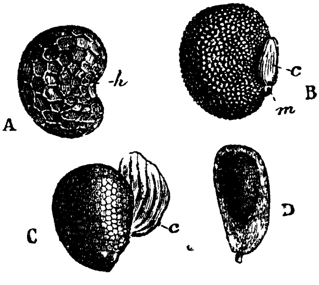


FIG 604.—*A*, Seed of *Papaver Rhoeas*, *h*, the hilum. *B*, Seed of *Corydalis ochroleuca*; *m*, micropyle; *c*, caruncula. *C*, Seed of *Chelidonium majus*. *D*, Seed of *Nymphaea alba* with its arillus. (After DUCHARTRE)

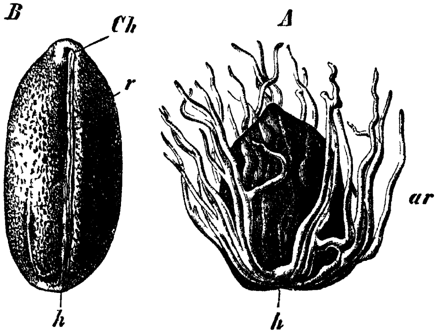


FIG. 605.—*A*, *Myristica fragrans*, seed from which the arillus (*ar*) is partly detached *B*, *Myristica argentea*, seed after removal of the arillus; *Ch*, chalaza; *r*, raphe; *h*, hilum (After WARBURG. ¾ nat. size.)

According to the nature of the pericarp the forms of fruit may be classified as follows:

1. A fruit with a dry pericarp, which opens when ripe, is termed a CAPSULE (Fig. 607). When dehiscence takes places by a separation of the carpels along their lines of union, the capsule is SEPTICIDAL (*e.g.* *Colchicum*, Fig. 830); when the

separate loculi open by means of a longitudinal split, it is termed LOCULICIDAL (*e.g. Ornithogalum*, Fig. 832), and when definite circumscribed openings are formed it is termed PORICIDAL (*e.g. Paparer*). As special types of frequent occurrence may be mentioned: the FOLLICLE, which is a capsule developed from a single carpel and opening by separation of the ventral suture, *e.g. Aconitum* (Fig. 677); the LEGUME or pod, which differs from the follicle in dehiscing by both ventral and dorsal sutures, *e.g.* Pea; and the siliqua of the Cruciferae, which opens by the separation of the carpels from the false septum (*e.g. Cheiranthus*, Fig. 683).

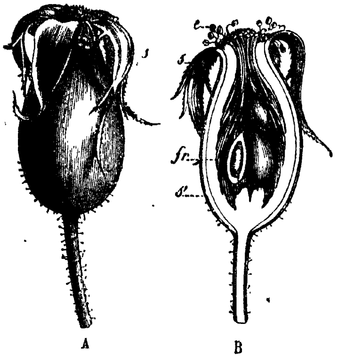


FIG. 606.—Collective fruit of *Rosa alba*, consisting of the fleshy hollowed axis *s'*, the persistent sepals *s*, and the carpels *fr*. The stamens *e* have withered. (After DUCHARTRE.)

2. INDEHISCENT FRUITS have a pericarp which does not open at maturity.

(*a*) Those with a hard pericarp are termed NUTS, *e.g.* Hazel-nut, Lime, *Helianthus*, *Fumaria*, *Fagopyrum* (Fig. 608).

(*b*) When a dry fruit, consisting of several carpels, separates at maturity into its partial fruits without the latter opening, it is termed a SCHIZOCARP (*e.g.* Umbelliferae, *Malva*, *Galium*, Fig. 609).

(*c*) A BERRY is a fruit in which all the layers of the pericarp become succulent, as in *Vaccinium*, *Vitis*, *Physalis* (Fig. 610).

(*d*) In the DRUPE the pericarp is differentiated into a succulent exocarp and a hard endocarp. *Prunus* (Fig. 697) and *Juglans* (Fig. 658) are familiar examples.

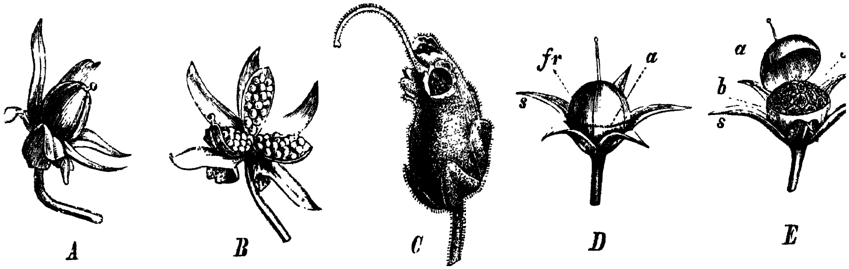


FIG. 607.—Modes of dehiscence of capsular fruits. *A*, *B*, Capsule of *Viola tricolor* before and after the dehiscence; *C*, poricidal capsule of *Antirrhinum majus* (magnified); *D*, *E*, pyxidium of *Anagallis arvensis* before and after dehiscence.

When, on the other hand, the group of fruits borne on an inflorescence has the appearance of a single fruit, the structure may be termed a SPURIOUS FRUIT. The Fig (*Ficus*) is the best-known example of this, but similar spurious fruits are especially frequent in the Urticaceae and Moraceae. The comparison of a Blackberry, which is the product of a single flower, with the spurious fruit of the Mulberry will show how closely the two structures may resemble one another (Fig. 611).

Distribution of Seeds (^{17b})

The same agents are available in the distribution of seeds as in the conveyance of pollen—currents of air and water, animals, and in addition human traffic. A distinction must be made, however, between the conveyance of pollen and of seeds, in that while a pollen-grain is extremely small and weighs very little, seeds contain a certain amount of reserve-materials and are thus larger and heavier. In spite of this the transport of seeds by the wind is the main means of their dispersal.

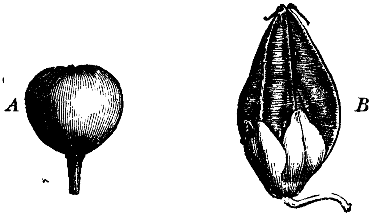


FIG. 608.—Dry indehiscent fruits. *A*, Nut of *Fumaria officinalis* (× 6). *B*, Of *Fagopyrum esculentum* (× 2). (After DUCHARTRE.)

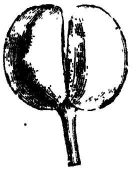


FIG. 609.—Schizocarp of *Galium mollugo*. (× 6. After DUCHARTRE.)

Often the suitability of seeds for wind-dispersal is due simply to their minute size and their lightness; thus millions of seeds are produced in a capsule of *Stanhopea*, and the weight of a seed of *Dendrobium attenuatum* has been determined to be about $\frac{1}{200}$ milligramme. Thus these Orchids play a part as epiphytes in damp tropical forests only equalled by Ferns, the spores of which are as light. A much more common arrangement is found in heavier seeds when the volume is increased and a large surface is offered to the wind. Either the whole surface of the seed bears longer or shorter hairs as in the Willow (Fig. 656), Poplar (Fig. 657), and Cotton (Fig. 728), or a longer tuft of hairs is borne at one end as in the Asclepiadaceae and Apocynaceae (*Strophanthus*, Fig. 774), and many Gesneriaceae and Bromeliaceae. An equally frequent arrangement in other families of plants is the development of a flat wing formed of a thin and light membrane. This in our Firs (Fig. 626) and Pines (Fig. 627) is split off from the ovuliferous scale, while in *Rhododendron*, Bignoniaceae, some Cucurbitaceae (*Zanonia*), and in the Rubiaceae

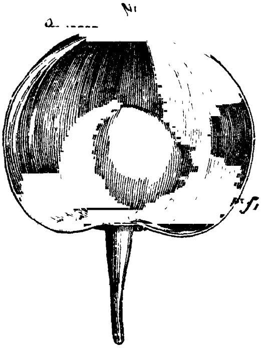


FIG. 610.—Fruit of *Physalis alkekengi*, consisting of the persistent calyx *s*, surrounding the berry *fr*, derived from the ovary. (After DUCHARTRE.)

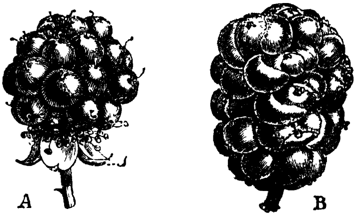


FIG. 611.—*A*, Collective fruit of *Rubus fruticosus*. *B*, Inflorescence of Mulberry (*Morus nigra*, spurious fruit. (After DUCHARTRE.)

(*Cinchona*, Fig. 794) it develops on each seed within the ovary. In no case is it more perfect than in *Pithecoctenium echinatum* (Fig. 612), where the delicate silky wing leads to the falling seed assuming an almost horizontal position and being carried far even by a slight breeze.

Other parts of the flower or fruit may be developed as wings, especially when one-seeded fruits (or schizocarps) are concerned. Examples of this are afforded by the sepals of the Dipterocarpaceae, the large bract of the inflorescence of the Lime (Fig. 730), the bract and bracteoles of *Carpinus* (Fig. 660), and more commonly the wall of the ovary as in *Betula* (Fig. 660), *Alnus*, *Ulmus* (Fig. 653), Polygonaceae (Fig. 649 *D*), *Acer* (Fig. 746), *Fraxinus* (Fig. 769), or the fruits of the Typhaceae, *Eriophorum* (Fig. 842) and *Anemone* (Fig. 675). The same use is served by the crown of hairs (pappus) which is developed at the upper end of one-seeded fruits such as those of the Valerianaceae (Fig. 796) and Compositae (Fig. 811 *B*), especially when it has a parachute-like form due to the later elongation of the upper end of the fruit as in *Taraxacum* (Fig. 812), *Tragopogon*, etc. According to DINGLER the fall in air as compared with that in a vacuum in the first second is six times slower in the case of the fruits of *Cynara Scolymus* provided with scaly hairs; in *Pinus sylvestris* the fall is seven times, and in *Pithecoctenium* thirty times slower.

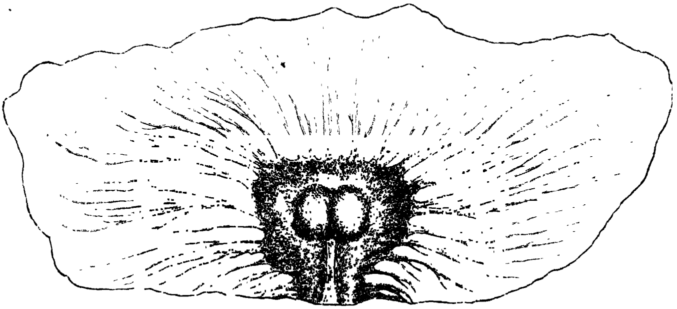


FIG. 612.—Winged seed of *Pithecoctenium echinatum*. (After NOLL. Nat. size.)

The distribution of seeds and fruits by ocean currents is important for many plants. The strand-flora of the Malayan Archipelago, for example, consists, according to SCHIMPER'S investigations, exclusively of plants with floating fruits or seeds, the adaptations of which correspond more or less to those of the Coco-nut (Fig. 824), which is distributed everywhere on tropical coasts. A thick exocarp consisting of a coarsely fibrous tissue renders the fruit buoyant and protects the brittle and stony endocarp from being broken against the rocks and stones of the shore. A very similar structure is exhibited by species of *Barringtonia*, *Cerbera Odollam* (Fig. 613), *Terminalia catappa*, *Nipa fruticans*, and many smaller plants belonging to the shrubby and herbaceous vegetation of the dunes and strand. In all cases the capacity of floating for a long time without loss of power of germination is a condition of the distribution of the seeds and the success of the species. The necessity of both these capacities is illustrated by the limited distribution of the Palm, *Lodoicea Seychellarum*, which is capable of floating but cannot endure the effect of salt water.

The distribution of fruits and seeds by means of animals depends as a rule upon the succulent and attractive fruits serving as food for birds, the undigested seeds being shed. A familiar example is afforded by the Elder (*Sambucus nigra*), the black fruits of which are eaten by various birds in summer. There are many such cases, and for some seeds the passage through the intestine of the animal appears to be a necessary preliminary to germination. The development of an arillus (cf. p. 593) is in many cases an adaptation to distribute the seed by means of animals. The arillus of *Taxus* with its bright red colour which surrounds the single seed is greedily eaten by blackbirds ; the arillus is the only part of the tree that is not poisonous. The red fruits of *Euonymus* when they open expose four seeds with bright red arilli, which are eaten by chaffinches. The Nutmeg is distributed over the islands about the Moluccas by a large pigeon which is attracted by the bright red arillus around the black seed which is exposed on the dehiscence of the fruit. In a similar way our Mistletoe in winter, when little other food can be obtained, is eaten by blackbirds and other birds ; when the birds clean their beaks the seeds remain attached to the branches by reason of the viscid substance around them and are able to germinate in this position. The spread of plants with hooked fruits, etc., such as *Galium aparine*, species of *Lappa* (cf. Fig. 808 *a*), *Bidens*, *Xanthium*, etc., by means of the fur of quadrupeds ; the general distribution of water-plants from one pond to another by aquatic birds ; and the distribution of the Hazel-nut, etc., by means of squirrels, do not require detailed description. Lastly, the distribution of certain seeds by means of ants must be mentioned ; these animals are attracted to remove and accumulate the seeds by the abundance of oil in the tissue of appendages such as the caruncula.

It is a matter of general knowledge that man by his commerce and industry has exerted great influence on the distribution of food-plants and other plants of economic value. In this way the seeds of many weeds have been unintentionally distributed over the inhabited earth, a fact that could be illustrated by numerous examples.

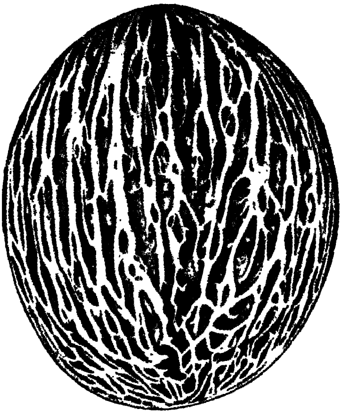


FIG. 613.—Fruit of *Cerbera Odollam*, from the drift. The exocarp and the succulent mesocarp are wanting, so that the buoyant tissue traversed by coarse fibrous strands is exposed. (After SCHIMPER.)

Germination [18]

Seeds which have escaped the various risks of distribution require a suitable environment for germination. Small seeds readily find shelter in cracks or depressions of the soil and become fixed there owing to special properties of their surface. Larger seeds are sufficiently covered by fallen leaves. The fruitlets of *Erodium* and other Geraniaceae, of *Avena sterilis*, species of *Stipa* and other Gramineae penetrate the soil by the aid of their hygroscopic curvatures (cf. p. 335, Fig. 276) ; the presence on their surface of backwardly-directed hairs prevents their losing the position reached. The burial of the fruits of *Arachis hypogaea*, *Trifolium subterraneum*, and *Okenia hypogaea* is brought about by the growth of their positively geotropic stalks, while negative heliotropism determines the insertion of the fruits of *Linaria cymbalaria* into the crevices of the walls on which the plant lives (cf. p. 353).

When the seeds find sufficient moisture they swell considerably. With this they lose some of their resistance to such dangers as extremes of temperature and desiccation; their former resistance was due to the small proportion of water they contained. The next step is the rupture of the seed-coat, which, as a rule, is effected by the emerging root. Since the root is always directed towards the micropyle, this region of least resistance is penetrated by the root-tip and forced open by the growth of the hypocotyl (Figs. 614, 615). The root at once bends downwards geotropically, and, by means of its root-hairs which are especially long and numerous at the junction of the root and hypocotyl, fastens the seedling in the soil. Meanwhile the hypocotyl grows and gradually emerges from the seed-coat, while the cotyledons, as a rule, remain for a time enclosed in the latter and absorb the remainder of the reserve-material (Figs. 614, 616*a*). This process leads to the hypocotyl becoming more and more strongly curved, and the tension resulting from its further growth withdraws the cotyledons from the seed-coat. The seedling then becomes erect, the leaves are expanded and can assimilate, and thus its independent life commences. The number of cotyledons is usually 2, but in some genera of Coniferae varies from 3-∞ (Fig. 615).

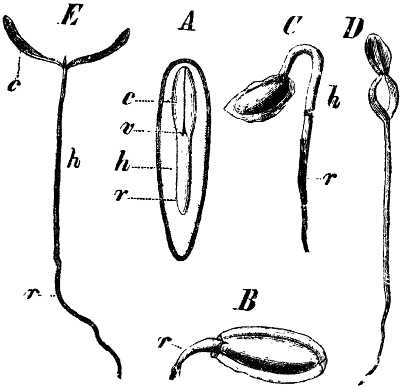


FIG. 614.—*Thuja occidentalis.* *A*, Median longitudinal section of the ripe seed. *B-E* Stages in germination; *h*, hypocotyl; *c*, cotyledons; *r*, radicle; *v*, growing point of stem. (*A* × 5; *B*, *C* × 2; *D*, *E* nat. size. After SCHENCK.)

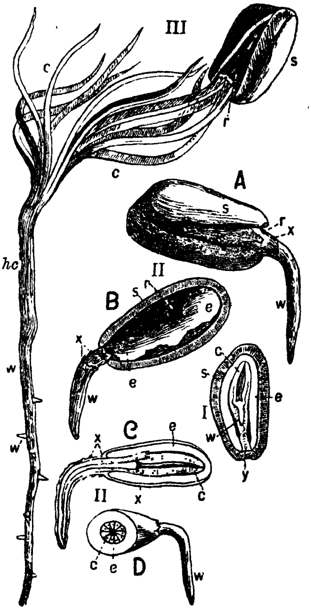


FIG. 615.—*Pinus pinea.* Germination. (After SACHS.) *I*, Longitudinal section of the seed; *y*, micropylar end. *II*, Early stage of germination; *s*, seed-coat; *e*, endosperm; *w*, primary root; *x*, broken-through embryo-sac; *r*, red layer of the seed-coat. *III*, The cotyledons (c) have escaped from the exhausted seed; *hc*, hypocotyl; *w'*, lateral roots.

This most frequent type of germination is characterised by the cotyledons being expanded above ground and is termed EPIGEAL. It is nearly always found in the case of small seeds.

HYPOGEAL germination is for the most part found in large-seeded Dicotyledons, the cotyledons of which contain the stored reserve-materials (*e.g.* *Vicia faba*, *Pisum*, *Aesculus*, *Juglans*, etc.). It is characterised by the cotyledons remaining enclosed in the seed-coat after the root has penetrated into the soil ; the epicotyledonary stem emerges from between the cotyledons, becomes erect, and bears the later leaves in the usual way. While there is a sharp morphological distinction between the two types of germination, the difference is of little systematic value ; within the Papilionaceae many intermediate conditions are found, and in the genus *Phaseolus*, *Ph. vulgaris* is epigeal and *Ph. multiflorus* hypogeal.

The germination of monocotyledonous seeds differs from the cases described above in that after the main root has emerged the sheathing base of the larger or smaller cotyledon emerges from the seed. Its tip remains either for a time or permanently in the seed, and serves as an absorbent organ to convey the reserve-materials stored in the endosperm to the seedling. The first leaf of the latter soon emerges from the sheathing base of the cotyledon (Fig. 616 *b*). Very hard seed-coats are often provided with special arrangements to enable the root to escape. Thus in the coco-nut three openings are present, one corresponding to each carpel. The opening behind which the tip of the root of the single embryo is situated is covered by a very thin layer, while the two other openings are firmly closed. The hard stony seed-coat of another Palm (*Acrocomia sclerocarpa*) has a loosely fastened plug opposite the tip of the root. In the whole family of the Scitamineae there is a limited thinner region of the hard seed-coat above the root-tip of the embryo, which is lifted up as a sort of lid on germination.

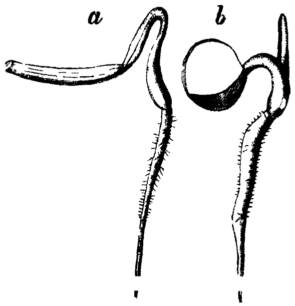


FIG. 616. — Seedlings, *a*, of *Scorzonera humilis* ; *b*, of *Iris pseudacorus*. (After KLEBS.)

The so-called "viviparous" plants show peculiar arrangements which can only be briefly mentioned here (Fig. 715). Vivipary is found in the inhabitants of tropical mangrove-swamps and is to be regarded as an ecological adaptation to the conditions of life. The one-seeded fruits germinate while still attached to the parent-plant, *i.e.* the pericarp is ruptured by the radicle of the embryo which first grows from the micropylar end of the seed. The hypocotyl which thus becomes free may attain the length of over 1 metre in *Rhizophora* (cf. Figs. 182, 715). The embryo thus hangs by its absorbent cotyledons which remain in the seed, until it separates from the plant owing to its own weight, and, falling vertically, sticks into the soft mud.

Arrangement of the Classes, Orders, and Families

CLASS I

Gymnospermae (^{19})

Of the groups of Gymnosperms the Cycadeae can certainly be traced back to the Cycadofilices (cf p. 537, Pteridospermeae), probably by way of the Bennettitaceae (cf. p. 618, *Cycadeoidea*) ; as regards the Coniferae, however, it is a matter of doubt whether they stand closer to the Lycopodiinae or to the Cycadinae. While on account of the vegetative organs, the former view could be entertained, the cone-like flowers of the Coniferae seem clearly to point to a close connection with the

Cycadinae. The cones of the Abietineae consist, like those of the Cycads, of numerous macrosporophylls. Each cone corresponds to a flower, and not to an inflorescence, just as is the case for the spirally constructed flower of the Magnoliaceae.

Order 1. Cycadinae (11)

This includes the single Family **Cycadaceae.** These are woody plants restricted to tropical and sub-tropical regions. *Cycas* is a native of Asia; *Macrozamia* and *Bowenia* of Australia. *Encephalartos* and *Stangeria* are African, while America has the genera *Dioon*, *Ceratozamia*, *Zamia*, and *Microcycas*. The general habit is illustrated by the fine examples of *Cycas revoluta* in Fig. 617, some of which are branched.

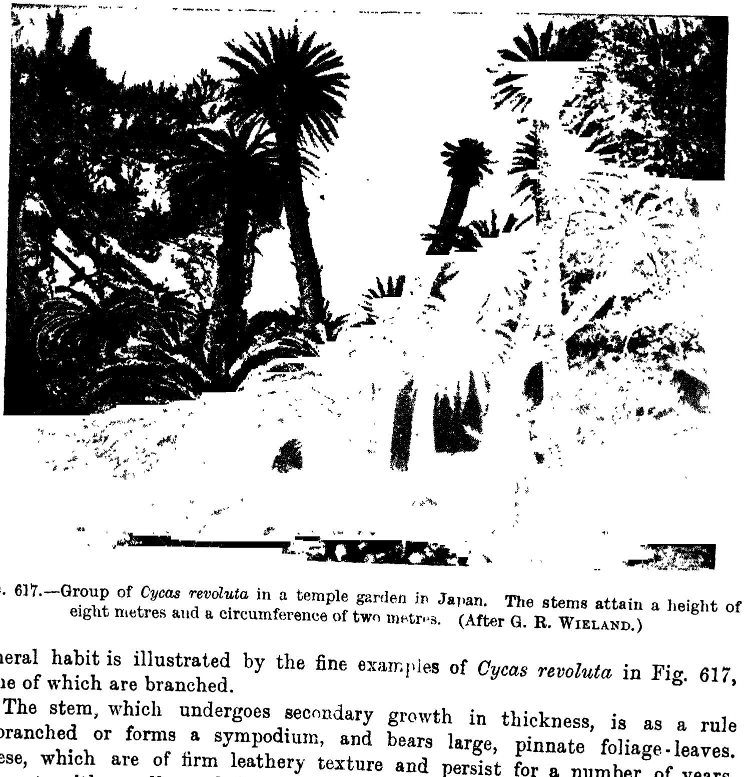


Fig. 617.—Group of *Cycas revoluta* in a temple garden in Japan. The stems attain a height of eight metres and a circumference of two metres. (After G. R. Wieland.)

The stem, which undergoes secondary growth in thickness, is as a rule unbranched or forms a sympodium, and bears large, pinnate foliage-leaves. These, which are of firm leathery texture and persist for a number of years, alternate with smaller scale-leaves and form a large terminal crown. The surface of the cylindrical or tuberous stem is clothed with the scale-leaves and the bases of the old foliage-leaves. Mucilage ducts are present in all parts of the plant. The vascular bundles are collateral, but their xylem consists of tracheides only.

The Cycadaceae are dioecious. Fig. 618 represents a female plant of *Cycas revoluta*, in which the growing point forms alternate zones of foliage-leaves and macrosporophylls. When young the foliage-leaves are rolled up circinately as in the Ferns. One of the sporophylls is represented in detail in Fig. 618*a*. It shows the pinnate form of the foliage-leaf, but is densely covered with brown hairs, and chlorophyll is wanting. Towards the base two to eight macrosporangia are borne on the margins, in the place of pinnae. It is evident that each female plant of *Cycas* which has reached the flowering condition exhibits a regular succession of flowering and vegetative periods. The flower represented by the group of sporophylls is always grown through by the further development of the apex, which as a rule does not branch. The male plant of *Cycas* and the other Cycadaceae bear their sporophylls in terminal cones, often of great size, while the further growth of the plant is effected by a lateral bud which continues the direction of growth of the sympodial axis, displacing the cone to one side.

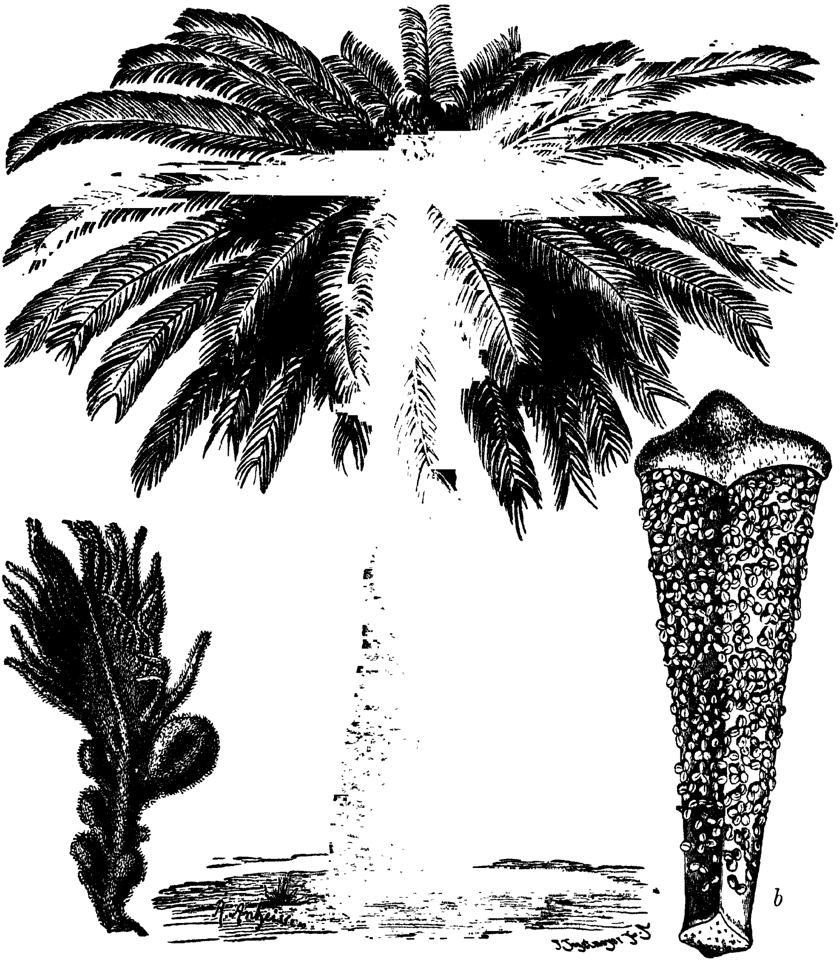


FIG. 418.—*Cycas revoluta*, female plant in flower. (From a photograph.) *a*, Macrosporophyll (carpel) of *Cycas revoluta*. (After SACHS.) *b*, Microsporophyll (stamen) of *Cycas circinalis*. (After RICHARD.)

The cones consist of numerous sporophylls arranged spirally on the axis. The microsporophylls bear large numbers of microsporangia on the lower surface (Fig.

618*b*). The macrosporophylls of the cone-bearing Cycadaceae are considerably modified as compared with *Cycas*, and each bears two marginal macrosporangia (Fig. 619). For the developmental history cf. p. 572.

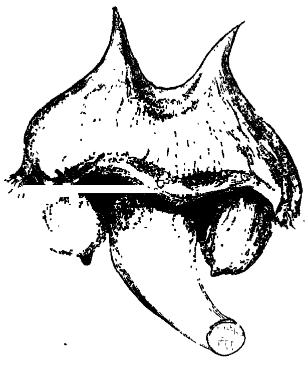


FIG. 619.—*Ceratozamia robusta*. Macrosporophyll with two macrosporangia. (After GOEBEL.)

Order 2. Ginkgoinae (11)

The single representative of the Family of the **Ginkgoaceae** which forms this order is *Ginkgo biloba*. This tree comes from Japan, but is often seen in cultivation in Europe. The long-stalked leaves are divided dichotomously into two or more lobes and are shed annually. The flowers are dioecious. The numerous stamens are situated on an elongated axis which bears no enveloping leaves. Microsporangia with an "endothecium" (cf. p. 554). Macrosporangia in pairs at the summit of short shoots; sporophylls reduced to a collar-like outgrowth around the base of the sporangium (Fig. 620). Developmental history, cf. p. 572.

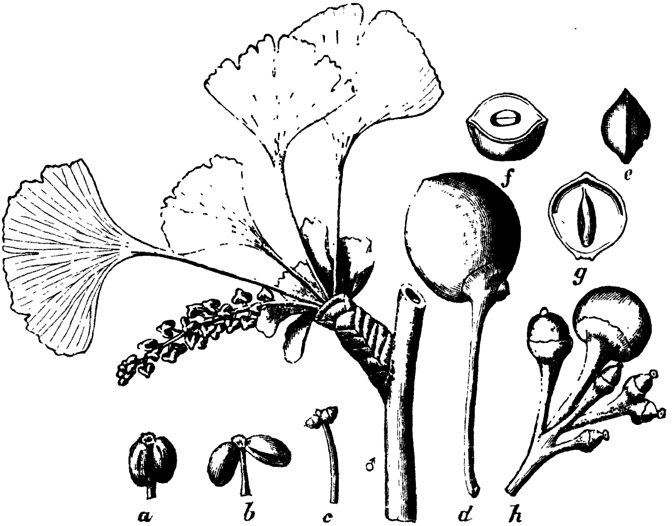


FIG. 620.—*Ginkgo biloba*. Male branch with flower; the leaves are not yet full-grown. *a*, *b*, Stamens; *c*, female flower; *d*, fruit; *e*, stone of same; *f*, stone in cross-section; *g*, in longitudinal section showing the embryo; *h*, female flower with an exceptionally large number of ovules borne on separate stalks. (Male flower and *c*, nat. size; *d*, slightly reduced; the other figures magnified. After RICHARD; *a*-*d* after EICHLER.)

Order 3. Coniferae (12)

The Coniferae include conspicuous trees or shrubs with woody stems. The possession of small, undivided, firm leaves, flat or needle-shaped, of xeromorphic structure, and usually lasting for several seasons, is a common character of the plants of the order; they thus, with a few exceptions, such as the Larch, belong to the evergreen vegetation. All Conifers are profusely branched, and a distinction into long and short shoots is evident in the genera *Pinus*, *Larix*, and *Cedrus*. In all cases the direction and rapidity of growth of the main

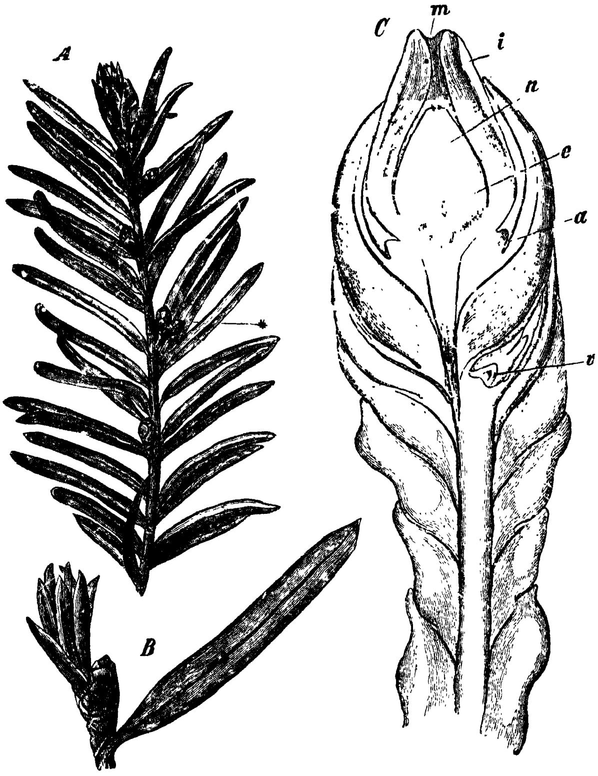


FIG. 621.—*Taxus baccata*. *A*, branch with female flowers; *, two ovules on the same shoot (nat. size). *B*, Leaf with axillary, fertile shoot (× 2). *C*, Median longitudinal section of a primary and secondary shoot; *v*, vegetative cone of the primary shoot; *a*, rudiment of the aril; *e*, rudiment of the embryo-sac; *n*, nucellus; *i*, integument; *m*, micropyle (× 48). (After STRASBURGER.) *POISONOUS.*

axis differs from that of the lateral branches. This is especially seen in young individuals; old trees are often more irregular in outline.

The absence of vessels from the xylem of young plants and from the secondary wood is an anatomical characteristic. Their place is taken by large tracheides with peculiar bordered pits on the radial walls; these form a very uniform wood. The majority of the Coniferae have resin abundantly present in all the parts of the plant.

The Coniferae in contrast to the Cycadinae are mostly inhabitants of temperate regions, and are among the trees which approach nearest to the polar regions. Within the tropics they are mostly confined to mountains.

The Coniferae are divided into two families on account of differences in the floral structure.

The *Taxaceae* have female flowers with one or few macrosporangia; the latter are usually provided with an arillus. The flowers are usually not definite cones. Mostly dioecious.

The *Pinaceae*, on the other hand, have a number of ovules in each female flower, the latter being a cone with numerous sporophylls borne on an axis. Arillus not present. Usually monoecious.

Family **Taxaceae.**—The plants belonging to this family are grouped in a number of small genera, some of which, such as *Taxus*, *Torreya*, and *Cephalotaxus*, occur in the northern hemisphere, but most are distributed in the southern hemisphere. The most important genus is *Podocarpus*, the numerous species of which are widely distributed in temperate East Asia and in Australia and New Zealand, and also occur as stately trees on the mountains of the Asiatic tropics. The female flowers are small shoots, the sporophylls of which are swollen and succulent; one or two sporophylls bear at the summit a single anatropous ovule surrounded by a fleshy arillus. The male flowers, which are borne on the same or on distinct individuals, are small, erect cones consisting of numerous sporophylls attached to a short erect axis. Each sporophyll bears two microsporangia on the lower surface; the microspores are provided with distended wings.

Taxus baccata is the only European representative of the family. The Yew, which is now for the most part artificially introduced, had formerly a wide distribution as an evergreen undergrowth in our native woods (Figs. 621, 622). The Yew tree attains a height of 10 m. Isolated examples of large size occur. All the branches are shoots of unlimited growth. The leaves stand on all sides of the ascending main shoots, but in two rows on the horizontally-expanded lateral branches. They are narrow, flat leaves and persist for several years. The tree is dioecious; the flowers are situated on the lower surface of the twigs and arise in the axils of the leaves of the preceding year. The male flowers are invested at the base by a number of scale-leaves and contain some ten peltate stamens, each of which bears 5-9 pollen-sacs (Fig. 622 *A*). The mode of opening of the sporangia is peculiar. The outer wall splits at the base and along the side of each pollen-sac, so that the whole stamen resembles an umbrella turned inside out; the pollen remains for a time in the pocket-like depressions, from which it is removed by the wind. The female flower (Fig. 621) usually develops singly as a secondary, axillary shoot of the uppermost scale-leaf of a primary shoot; the apex of the latter is displaced to the side and does not develop further. Each flower consists of a single atropous ovule with one integument. The drop of fluid excreted from the micropyle of many Gymnosperms is especially well shown by the Yew. As the seed develops, a fleshy arillus springs from its base and surrounds the mature seed like a bright red cup. The foliage and seed are poisonous, but the aril, which induces birds to distribute the seed, is harmless.

Family **Pinaceae.**—This family includes the most important Coniferae, and on grounds of differences in leaf-arrangement and in the position of the ovules is divided into two sub-families. The forms with the leaves opposite or in whorls are included in the *Cupressineae* ; they also have the ovules erect. All the forms with alternate leaves are included in the *Abietineae*, and, almost without exception, they also possess inverted ovules.

Sub-family **Cupressineae.**—Some of the Cupressineae have needle-shaped leaves in whorls (Juniper, Fig. 623) ; others have decussately-arranged, scale-like leaves (*Thuja*, *Juniperus sabina*). The former type is to be regarded as the more primitive, for the seedlings of *Thuja* have needle-shaped leaves, and individual branches of scale-leaved forms of *Juniperus* revert to the needle-shaped leaves in whorls of three.

The Cupressineae, with the exception of *Juniperus*, are monoecious. The male flowers of *Juniperus communis* stand in the leaf-axils. At their base are a number of small scale-leaves (Fig. 623 *A*, *a*), above which come several whorls of peltate sporophylls (*c*), bearing 2-4 microsporangia (*d*) on the lower surface. The sporangia open by a vertical slit parallel to the long axis of the sporophyll. The female flowers occupy a corresponding position. The scale-leaves at the base (Fig. 623 *B*) are succeeded by a whorl of carpels (*C*, *b*), each of which bears a single upright ovule in a median position (*c*). After fertilisation a succulent parenchymatous growth mainly of the basal portions of the sporophylls raises the seeds and presses them together, without, however, obliterating the central space altogether. The three

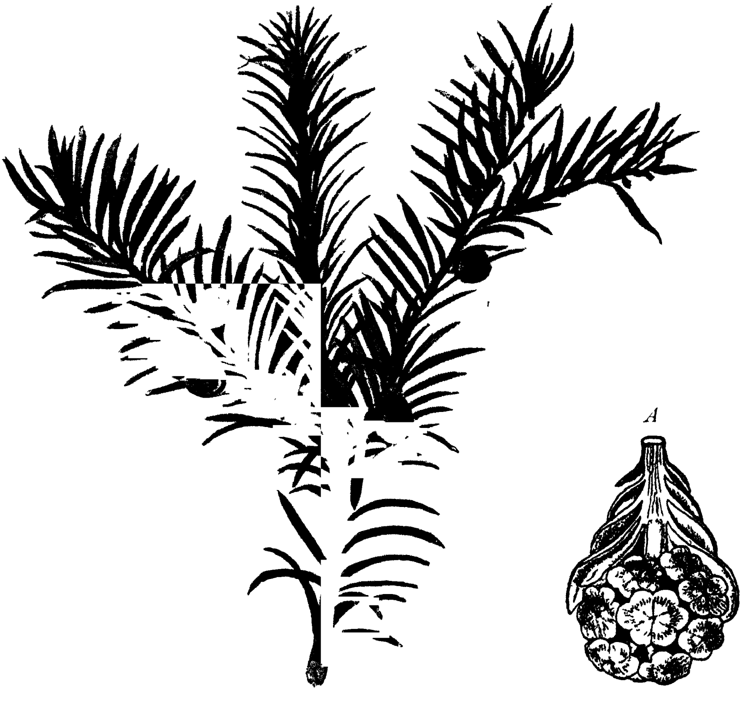


FIG. 622.—*Taxus baccata*, bearing fruits. (½ nat. size.) *A*, Male flower. (After RICHARD.) *POISONOUS.*

carpels become completely coherent above the seeds, but the place of union is still

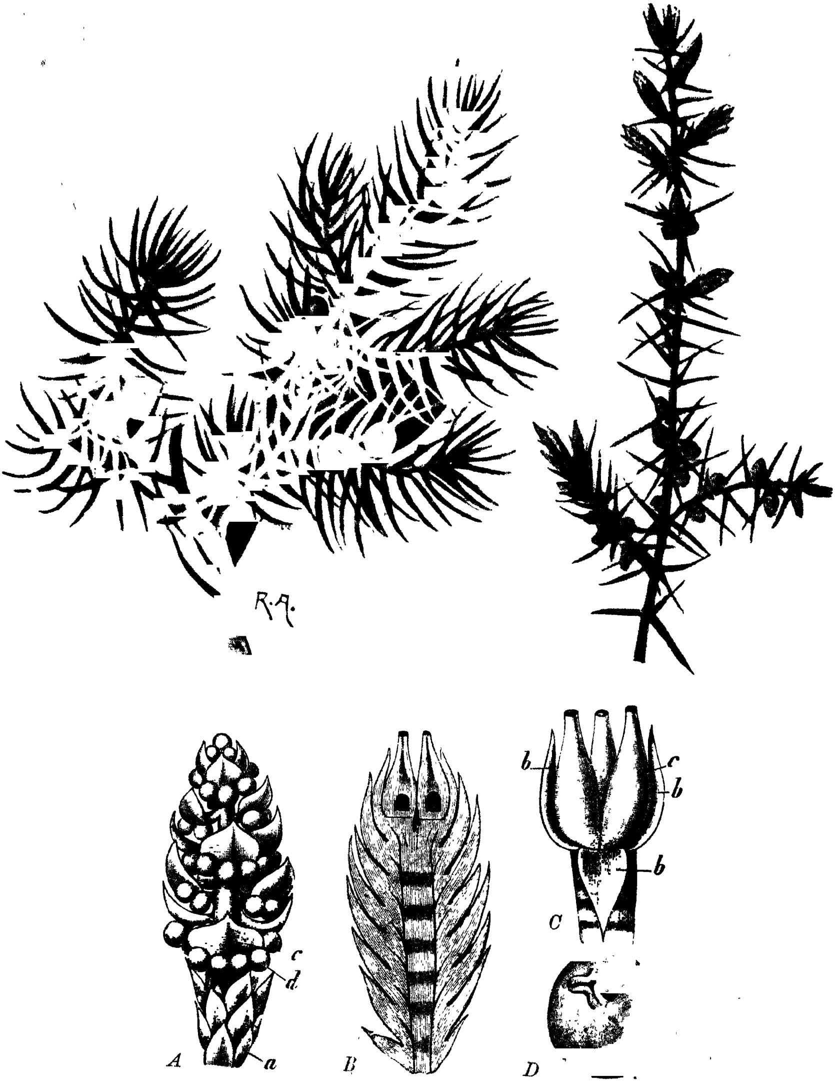


FIG. 623.—*Juniperus communis.* Twigs bearing fruits and male flowers. (⅔ nat. size.) *A*, Male flower ; *B*, fertile shoot with female flower ; *C*, female flower with one scale bent out of place ; *D*, fruit. (All magnified. After BERG and SCHMIDT.)

indicated by the scar at the apex of the ripe fruit. The succulence of the carpels gives the fruit the appearance of a berry. *Juniperus* is the only genus of the

Cupressineae with such fruits; the others, such as *Cupressus, Thuja, Taxodium*, have cones, and bear the ovules on a slight outgrowth of the scale.

Juniperus communis, Juniper, is a shrub or small tree distributed over the northern hemisphere. *J. Sabina*, a prostrate shrub of the Alps and other mountains of central and southern Europe The Cypress (*Cupressus sempervirens*) in the Mediterranean region. Species of *Thuja* are commonly grown as ornamental trees. *Taxodium distichum* is a deciduous tree, forming extended swampy woods on the north coast of the Gulf of Mexico from Florida to Galveston; the short shoots have two ranks of leaves and are shed as a whole. *T. mexicanum* is evergreen and is widely distributed on the highlands of Mexico; very large specimens occur, such as the giant tree of Tule, which at a height of 50 m. was 44 m. in circumference, and was estimated by VON HUMBOLDT to be 4000 years old (Fig 624).

FIG. 624 —*Taxodium mexicanum* in the churchyard of S. Maria de Tule at Oaxaka. This giant tree is one of the oldest living (From a photograph)

Sub-family **Abietineae.**—The floral structure of the Abietineae may be described in the first place. The male flowers (cf. p. 551) consist of an axis bearing scale-leaves at the base, and, above this, numerous stamens; the pollen-sacs (microsporangia) are situated on the lower surface of the stamen. In the Abietineae in the narrower sense there are two pollen-sacs, but in *Agathis* and *Araucaria* there are 5-15. The microspores are usually winged. The female flowers are always cones, consisting of an axis bearing the closely approximated scales, which protect the ovules. In *Agathis* and *Araucaria* each scale bears a single anatropous ovule at its base. The condition of affairs in *Sequoia* and *Sciadopitys* is similar, but the outgrowth is more clearly defined; each scale bears 4-9 anatropous ovules. In the Abietineae proper the limits of the two scales are still more marked. The two anatropous ovules are borne on an inner scale, which, at its base, is continuous with the scale of the cone. THE OUTER SCALE IS CALLED THE BRACT-SCALE, THE INNER THE OVULIFEROUS SCALE (Figs. 625 *C*, 626, *5*). The ovuliferous scale is the more strongly developed, and it is the part that becomes lignified and affords protection to the ovules. Even at the period of flowering the bract-scale is usually concealed by the ovuliferous scale and only to be detected on close inspection. In other forms, however (*e.g. Abies*, Fig. 625, *Pseudotsuga Douglasii*, etc), the bract-scales even in the older cone project prominently between the ovuliferous scales.

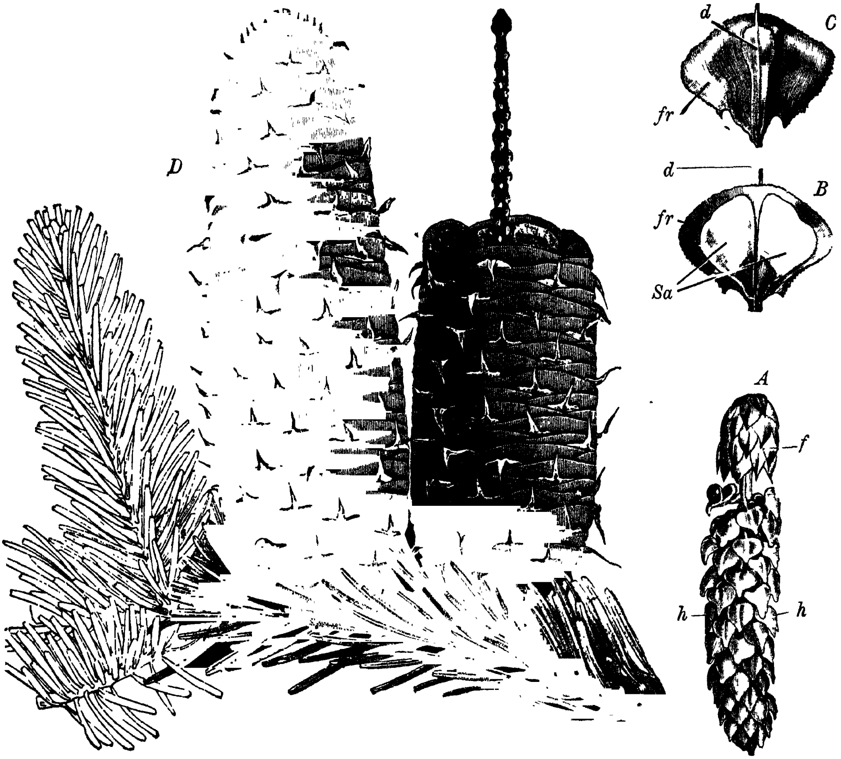


FIG. 625.—*Abies pectinata*. *A*, Male flower; *f*, scale-leaves, *h*, sporophylls. *B*, Bract-scale (*d*) and ovuliferous scale (*fr*), seen from above. *C*, The same from below, *sa*, the winged seeds. (After BERG and SCHMIDT.) *D*, *Abies Nordmanniana* with ripe cones, the scales in part shed. (Reduced from ENGLER and PRANTL.)

Most important Genera and Species.—*Agathis* (*Dammara*) is distributed in the Malayan Archipelago and extends to New Zealand; *A. australis* and *A. Dammara* yield Kauri Copal but no Dammar Resin; *Araucaria brasiliana* and *A. imbricata* are stately S. American forest trees. The genus *Sequoia* includes the most gigantic trees known; specimens of *S. gigantea* from the Californian Sierra Nevada attain a height of 100 m. and a diameter of 12 m. The beautiful *S. sempervirens* from the coastal mountains is hardly inferior in size.

The Silver Fir (*Abies pectinata*, Fig. 625 *A-C*) is a native of the mountains of the middle and south of Europe. It bears only long shoots. The flat, needle-like leaves, marked below by two white lines and emarginate at the tip, are borne on all sides of the axis, but are twisted into a horizontal position on the branches illuminated from above. They live for 6-8, or even for 15 years. The male flowers stand in the leaf-axils on the under side or on the flanks of the shoot, and grow downwards so that the pollen-sacs are directed upwards. The wall of the sporangium opens by an obliquely longitudinal split, which gapes widely and allows the winged microspores to escape. The female flowers arise from the upper side of a branch and are directed vertically upwards. The bract-scales are longer than the broad, ovuliferous scales. The fertilised cones retain the upright position, and when ripe the scales separate from the axis and so set the seeds free from the plant. The development of the seeds takes a year. *Abies Nordmanniana* from the Caucasus (Fig. 625 *D*), *A. concolor*, *A. balsamea*, and *A. nobilis* from North America are in cultivation.

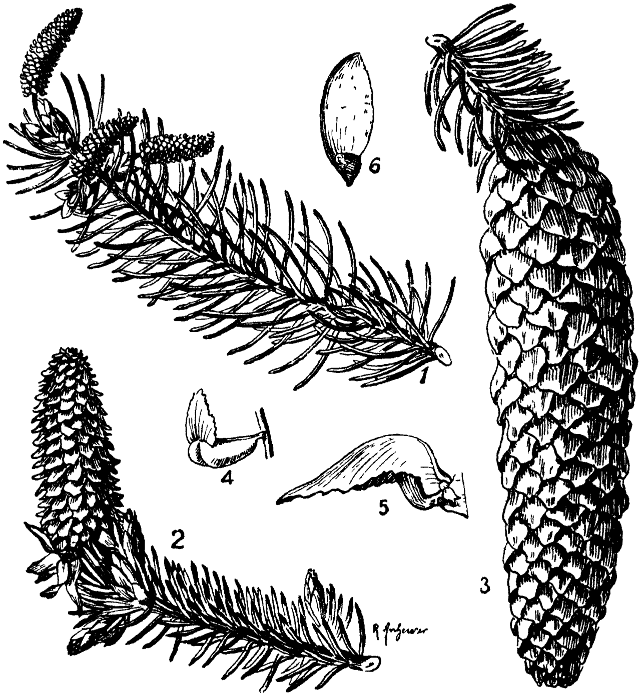


FIG. 626.—*Picea excelsa* (½ nat. size). *1*, Twig with male flowers. *2* Terminal female flower *3*, Pendulous cone *4*, Microsporophyll. *5*, Macrosporophyll, the bract-scale is covered by the large, bent-back, ovuliferous scale; an ovule is visible at the base of the ovuliferous scale. *6*, Ripe seed with the wing formed by a detached portion of the ovuliferous scale. (× 4 6)

Picea excelsa, the Spruce (Fig. 626), is a fine tree of pyramidal shape; it has no short shoots, and the long shoots bear on all sides pointed, quadrangular, needle-shaped leaves, which on horizontal or pendulous branches stand more

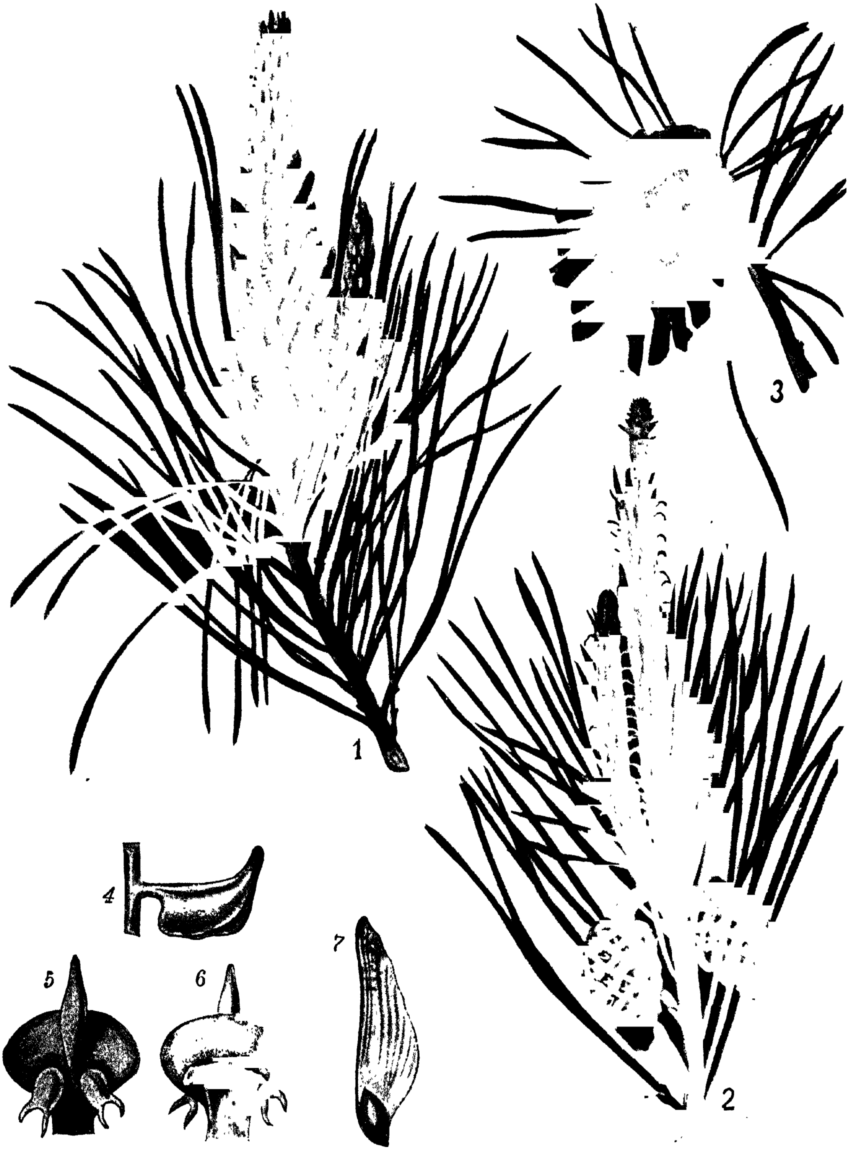


FIG. 627.—*Pinus sylvestris* (⅔ nat. size). *1*, Shoot of unlimited growth bearing short shoots; at the top the shoot of the current year. At the base of the latter are numerous male flowers each in the place of a short shoot, and nearer the tip brown scale-leaves, in the axil of each of which is a short shoot. *2*, Similar branch bearing a young female flower at the summit of the shoot of the current year, in place of a branch of unlimited growth. Two dependent green cones are borne on the shoot of the preceding year. *3*, Cone of the year before last, opened to allow of the escape of the seeds. *4*, A microsporophyll. *5*, Macrosporophyll from the adaxial side showing the ovuliferous scale with the two ovules at the base. *6*, Macrosporophyll from the abaxial side showing the small bract-scale below the large ovuliferous scale. 7, Ripe seed with its wing derived from the superficial layers of the ovuliferous scale. (× 4-7.)

or less erect. They live for 5-7 years, and on main shoots for 12 years. Male flowers as a rule on shoots of the previous year; on flowering they become twisted into an erect position. The two pollen-sacs open by a longitudinal slit. Female flowers terminal on the shoots of the previous year, usually near the summit of the tree. They stand erect at the time of flowering. The ripe cones are pendulous and, after setting free the seeds from between the scales, fall in pieces. The development of the seeds is completed in one year. *Picea orientalis* from Asia Minor, *Picea omorica* from Serbia, and *Picea alba*, from North America, also *Picea Engelmanni* and *Picea pungens* are frequently cultivated.

Larix europaea, the Larch (Fig. 628), is one of the few deciduous Conifers and replaces its foliage annually. There is a differentiation into long and short shoots. The former bear the narrow linear leaves, which are not xeromorphic, on all sides and continue the branching of the pyramidal tree, the lower branches of which often droop downwards. The short shoots arise in the axils of the leaves of the long shoots of the preceding year, and bear a rosette of 30-40 leaves which are somewhat shorter but resemble those of the long shoots. The flowers occur in a position corresponding to that of the short shoots. The male flowers are bent downwards when fully developed, and the opening of the upwardly directed pollen-sacs occurs as in *Abies*. The erect female cones produce seed in the same year. Species of *Cedrus* are evergreen forest trees from the Atlas Mountains, Lebanon, and the Himalayas, and are grown in pleasure grounds.

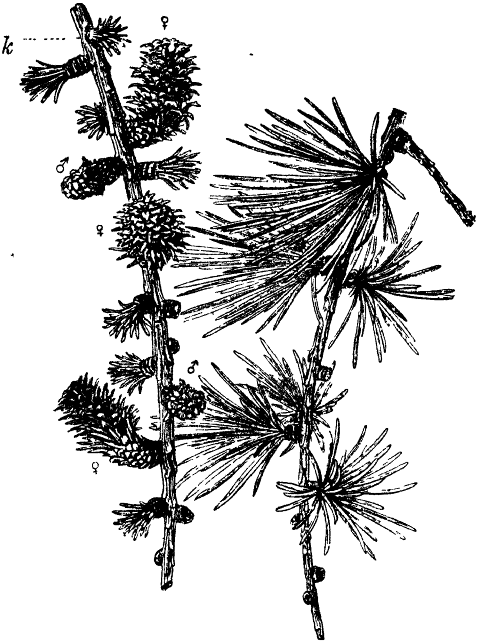


FIG. 628.—*Larix europaea.* Long shoots of the preceding year, that on the right bearing vegetative short shoots and that on the left male and female flowers in place of them. (From ENGLER and PRANTL.)

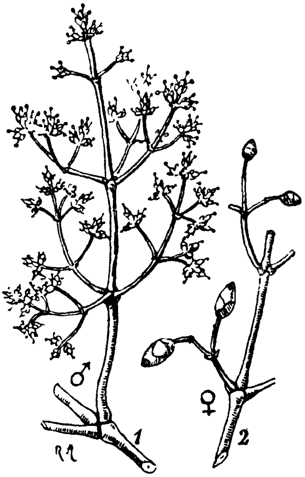


FIG. 629.—*Ephedra altissima.* *1*, Habit of a male inflorescence. *2*, An inflorescence with unripe fruits. ($\frac{2}{3}$ nat. size.)

The most advanced differentiation of the vegetative organs is found in the genus *Pinus*; *P. sylvestris*, the Scotch Fir, will serve as an example (Fig. 627).

Young seedlings in the first or second year have long shoots bearing needle-shaped leaves. On older plants this type of foliage is lost; the needles are replaced by colourless, membranous scale-leaves in the axils of which stand the short shoots

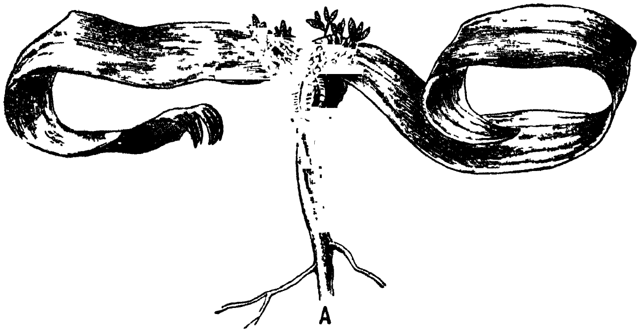


FIG. 630.—*Welwitschia mirabilis.* Young plant (from ENGLER and PRANTL).

(cf. the explanation of Fig. 627). The needles are shed in three years. The seeds ripen in the second year, and are set free by the separation of the scales of the cone, which till then have been closely pressed together. The cones subsequently are shed. *Pinus montana*, a dwarf Pine occurring on mountains; *P. pinea*, *P. cembra*, with edible seeds; *P. laricio*, Corsican Pine from Austria; *P. Pinaster*, Maritime Pine from the Mediterranean region; *P. taeda*, *P. Strobus*, Weymouth Pine, *P. Lambertiana* from North America.

POISONOUS.—*Juniperus Sabina*, *Taxus baccata*.

OFFICIAL.—*Juniperus oxycedrus* yields OLEUM CADINUM; *Juniperus communis*, OLEUM JUNIPERI; *Abies balsamea* supplies TEREBINTHINA CANADENSIS; *Abies sibirica* supplies OLEUM ABIETIS; *Pinus* sp. produce OLEUM TEREBINTHINAE RECTIF.

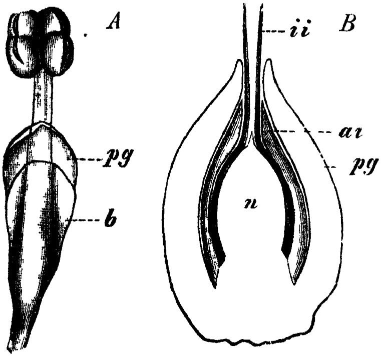


FIG. 631.—*A*, *Ephedra altissima.* Male flower (× 16, after STRASBURGER); *pg*, perigone *b*, leaf. *B*, *Gnetum Gnemon* longitudinal section of a female flower (× 32, after LOTSY), *n*, nucellus; *ii*, inner, and *ai*, outer integuments; *pg*, integument-like investment or perianth.

Order 4. Gnetinae (13, 19a)

The only Family in this order is that of the **Gnetaceae**, to which only three genera belong: *Ephedra* (Fig. 629), leafless shrubs of warm, dry regions of the northern hemisphere. *Welwitschia mirabilis* (Fig. 630), a monotypic plant from the deserts of South-West Africa; the widely expanded summit of the stem bears after the cotyledons only a single pair of leaves, which are 1 m. in length and continue to grow at their bases. *Gnetum* (Fig. 632), tropical trees or climbers with broad, reticulately-veined leaves. These genera, while differing widely in appearance, agree in possessing opposite leaves (in *Ephedra* reduced to scales), in the development of vessels in the secondary wood, the absence of resin canals, and in the presence of a perianth to the flowers, which are usually dioecious (Fig.

631). The possession of this perianth makes it impossible to regard the cones of the Gnetaceae as flowers. They are rather inflorescences and not homologous with the cones of the Coniferae. These points of agreement with both Gymnosperms and Angiosperms make the group in many ways an intermediate one between the two classes. The occasional or regular presence of flowers of both sexes in the inflorescences is noteworthy. Insects visit the flowers of all three genera, though they are as yet only known to effect pollination in the case of *Ephedra campylopoda*. On the development of the sexual generation cf. p. 581.

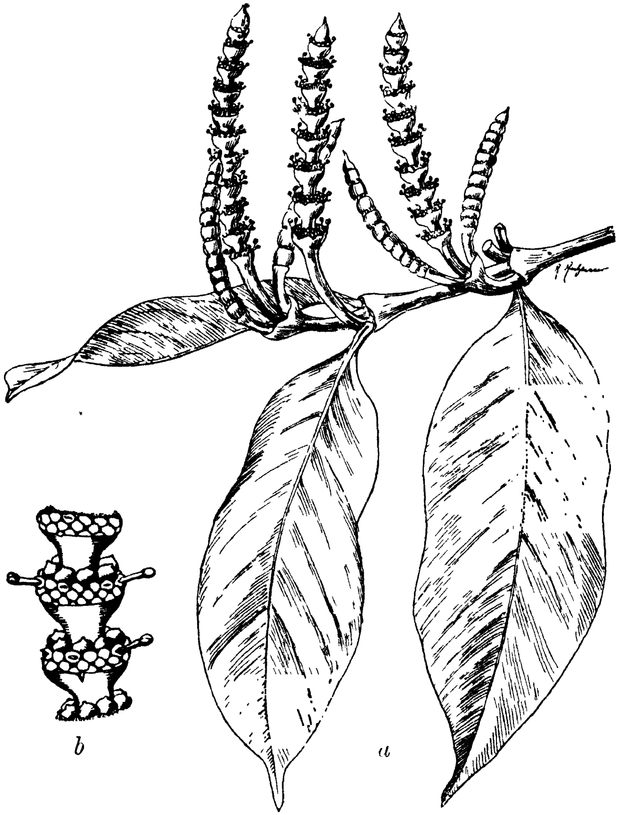


FIG. 632.—*Gnetum Gnemon* a, Branch with male inflorescences. b, Two whorls (× 2), consisting of numerous, acropetally-placed whorls, each of which bears above the spirally-arranged male flowers a whorl of (functionless) female flowers. (½ nat size) b, Whorls of flowers (× 2).

Fossil Gymnosperms (20)

According to D. H. SCOTT the most ancient seed-plants are those known from the Devonian; they attained great importance in the Carboniferous period. To the former period belong the fossil trees from Gilboa in the State of New York. The stems measure about 1 m. in diameter; portions with the bases of the compound leaves still attached are known. The seeds, enclosed in a cupule-like structure, are borne in pairs at the ends of slender forked branches Two species of the genus, which is known as *Eospermatopteris*, are distinguished *Aneurophyton elberfeldense* of similar habit is described by KRAUSEL and WEYLAND from the Middle Devonian of Elberfeld *Palaeopitys Milleri*, which has been regarded as

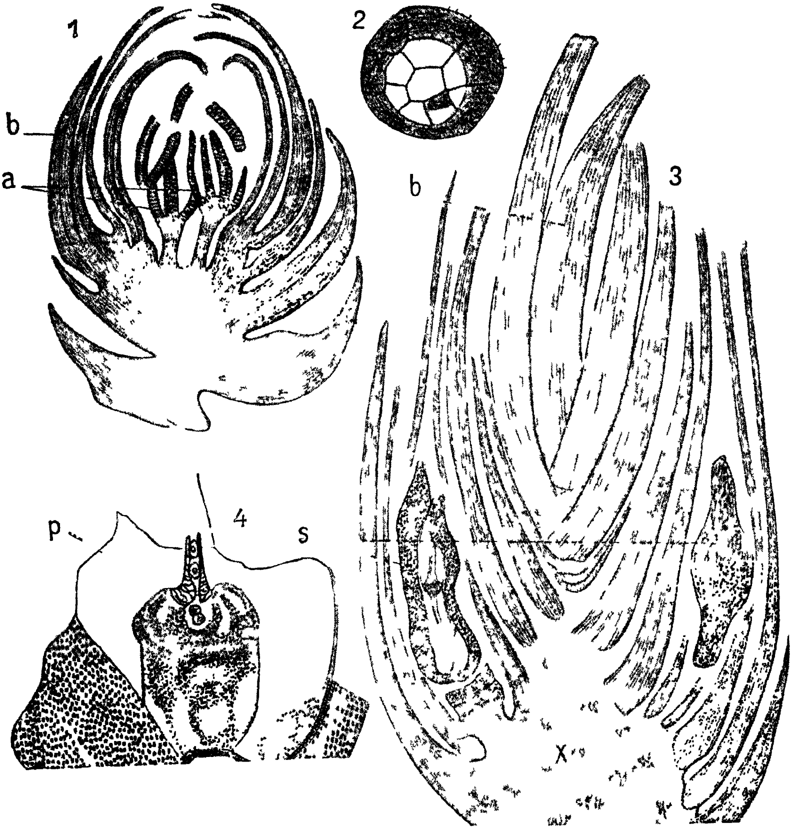


FIG 633 —*1 Cordaites subglomeratus* longitudinal section of a male flower-bud, *b* investing bracts *a*, stamens with several anthers *2* A pollen-grain, the prothallial cell is separated by a curved wall while the rest of the grain is divided into a number of cells *3 C Williamsoni* longitudinal section of a female inflorescence, *b* leaves, *s*, seed in longitudinal section *4*, *C Grand Euryi* longitudinal section of an ovule showing the deep pollen chamber in the nucellus containing a number of pollen-grains (After RENAULT)

the wood of a "coniferous tree from the Middle Old Red Sandstone of Scotland, has been recently re investigated by KIDSTON and LANG

The oldest seed plant so far discovered may perhaps be *Cladoxylon scoparium*, described by KRAUSEL and WEYLAND The stems of this bore spirally arranged leaves which attained a length of 18 mm and were deeply incised or dichotomously divided The sporophylls were fan shaped with a deeply lobed margin Each lobe appears to have borne a single spherical sporangium *Callixylon*, from the Upper Devonian of Russia and North America has as highly organised secondary wood as existing Conifers and has thus completely Gymnospermous characters

From the Cycadofilices, stems with secondary growth in thickness and with fern-like foliage which have hitherto always been classed with the Pteridophyta, OLIVER and SCOTT have separated the **Pteridospermae**; these may be briefly characterised as fern-like seed-plants. They have been dealt with at the end of the Pteridophyta (p. 537).

Cordaitaceae.—*Cordaites* is a peculiar type confined to the Palaeozoic rocks. Owing to the excellence of the preservation of the remains, its morphology is as well known as that of the existing Gymnosperms. The Cordaitaceae were lofty, branched trees with linear or broad and lobed leaves with parallel venation. Their flowers differ considerably from those of recent Gymnosperms. The male and female flowers are borne on spike-like axillary inflorescences. The female flower consists of a single atropous ovule with some bracteoles at its base; these resemble the vegetative foliage-leaves (Fig. 633). At the summit of the nucellus is a deeply sunken pollen-chamber in which pollen-grains are often met with (4, *p*). The male flowers terminate small shoots that are surrounded by a number of sterile bracts and at the summit produce a number of stamens, each of which has 2-4 anthers (Fig. 633, 1). An important fact as bearing on the phylogeny of the group is the presence of a male prothallus as a small multicellular body (2). The ovules and seeds show great structural agreement with those of *Cycas*. While some less common fossils (*Cycadites*, *Dicranophyllum*) may be placed in the same group, *Cordaites* is the most richly represented type of Gymnosperm found in the Carboniferous rocks. Undoubted Cycadophyta make their appearance in the lower Rothliegende.

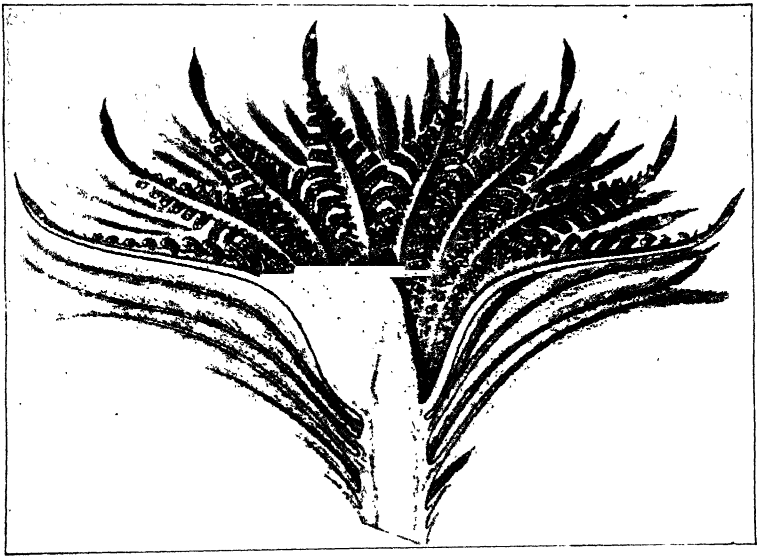


FIG. 634.—Reconstruction of the longitudinal section of the flower of *Cycadeoidea* (*Bennettites*) *ingens*. (From SCOTT after WIELAND.)

The Cordaiteae disappear in the lower Mesozoic strata. The Gymnosperm flora can be followed through the Trias, in which it consisted of extinct types of Cycadophyta, Ginkgoineae, and Coniferae, to the Jurassic period. In the latter it attained a great development in that both the Ginkgoineae and the Cycadophyta attained their maximum.

Bennettitaceae. — SCOTT has given an account of the appearance and the high degree of organisation attained by the Mesozoic Cycadophyta, from the knowledge obtained by WIELAND's study of the abundant material found in North America. The name *Cycadeoidea* proposed by the American author is synonymous with *Bennettites*; fruits derived from the hermaphrodite flowers were already imperfectly known from European strata under the latter name. The short and sometimes branched stems resembled recent Cycads in their appearance and foliage and bore flowers which were hermaphrodite and 12 cm. in length. A hundred or more spirally arranged perianth leaves surrounded a whorl of 18-20 microsporophylls, which were united at the base to form a deep cup, in the centre of which the gynaeceum arose (Fig. 634). The pinnate microsporophylls, 10 cm. in length, resemble the leaves of Ferns, and the microsporangia resemble the sporangia of the Marattiaceae. The gynaeceum consists of numerous long-stalked, atropous ovules which are surrounded and separated by scale-leaves: the micropyles, however, open freely on the exterior. The ripe seeds contained a highly developed dicotyledonous embryo and had no endosperm. They were protected and enclosed by the closely crowded outer ends of the scale-leaves (Fig. 635). Just as the Palaeozoic Pteridosperms combine the characters of Ferns and Gymnosperms, the flowers of the Mesozoic *Bennettites* or *Cycadeoidea* show a combination of characters of Angiosperms, Gymnosperms, and Ferns.

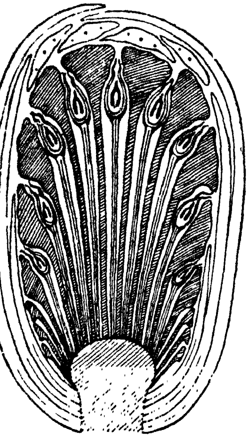


FIG. 635. — Longitudinal section of a fruit of *Bennettites Gibsonianus.* (After SCOTT.)

True Araucarieae appear in the Jurassic. In the Wealden, Cycadineae and Ginkgoineae along with some Coniferae were dominant among the Gymnosperms. On passing to the Cretaceous strata the ancient types are found to be reduced, while the Coniferae become more numerous. Among the latter appear existing genera (*Dammara, Sequoia, Pinus, Cedrus, Abies, Callitris,* etc.). The Taxaceae also appear to be represented, but the remains are of uncertain affinity.

The Tertiary Gymnosperms belong entirely to existing types and for the most part to existing species. The Coniferae are dominant; the Ginkgoineae are represented only by *Ginkgo biloba*, but this occurred in Europe along with other species now limited to Eastern Asia or North America (*Cryptomeria japonica, Taxodium distichum, Sequoia gigantea, S. sempervirens, Pinus Strobus,* etc.). One Cycadaceous plant (*Encephalartos*) is also known.

CLASS II

Angiospermae

1. Derivation of the Angiospermae from the Gymnospermae (21, 22)

The derivation of the Angiosperms from the Gymnosperms is one of the most difficult questions which it is necessary to consider here.

In 1923, when the preceding German edition of this text-book was published, the serodiagnostic method of MEZ and his botanical school was so far developed as to inspire the hope that it would result in an objective demonstration of the relationships of plants. The methods frequently employed in medical jurisprudence are based on the fact that morphologically related organisms will also show a chemical relationship of their albumens; this is seen, for instance, by a comparison of human blood with that of the anthropoid apes. It would follow from this that the expressed sap of related plants should give the same reaction when injected into the blood-vessels of the animals used in this type of investigation. Conclusions may then be drawn as to the degree of relationship of plants from the greater or less agreement of their proteid-reactions. It must, however, be premised for such conclusions to be sound that it is the reaction of the specific proteids (*i.e.* those characteristic of the species, genus, or family) which is being obtained, and not that of the reserve proteid substances, which can hardly be expected to show such differences for each species, etc.

The results of these methods, expressed in a large "Konigsberg phylogenetic tree," have in the interval been tested from various sides as MEZ himself had desired. These tests and critical examinations, among which those of R. VON WETTSTEIN (22) appear to be the most important, while fully recognising the value of a new method of investigation, are seriously critical of the results so far obtained. There is no sufficient proof that the SPECIFIC proteid substances are being employed in determining the relationships. Since this condition, the necessity of which has been referred to above, is not fulfilled or is only satisfied in some cases, the serodiagnostic method cannot be employed with certainty as the basis for a systematic arrangement. It will therefore be abandoned for this purpose here, though particular results will be taken account of where they agree with the conclusions obtained by the usual methods of systematic botany.

Further attempts to determine the origin of the Angiosperms by methods of comparative morphology may now be considered The view of WETTSTEIN (1) may in the first place be mentioned, that the flowers of *Casuarina*, regarded as the simplest angiospermic flower, may be connected with the inflorescence of *Ephedra* (Fig. 629). The male flower of *Casuarina* is derived from the male inflorescence of *Ephedra* in this way: the bracts give rise to the perigone; the bilocular anthers become united in pairs to give rise to quadrilocular stamens; an assumed increase in number of the stamens results in an arrangement in alternating whorls; and the formation of a corolla comes about by the transformation of stamens to petaloid staminodes. In a similar fashion the transformation of the ♀ inflorescence of *Ephedra* into a female flower is pictured. Further, the discovery of a species of *Ephedra* the ♂ inflorescence of which regularly terminates with some ♀ flowers opens the possibility of arriving at a hermaphrodite angiospermic flower. Since insects are known to be attracted by the drop of liquid secreted at the micropyle, an entomophilous, hermaphrodite angiosperm flower, rendered conspicuous by the bright yellow anthers, would result. This transition is morphologically possible and ecologically comprehensible; it leads to the Verticillatae (cf. the survey on p. 622), and through them to the Fagales. The further development from these forms is, however, a matter of difficulty. Support is sought for this line of transition from the occurrence of chalazogamy (cf. p. 587) and similar phenomena in the Fagales and associated families.

It can be objected to this theory that the families of Angiosperms assumed by WETTSTEIN to be lowest are not primitive, but reduced, and that other groups such as the Polycarpicae seem to stand much closer in floral construction to the Gymnosperms. The peculiar course of the pollen-tubes is met with in other groups, such as the Rosales; MURBECK (^{23}) has observed this in *Alchemilla arvensis*, and he concludes that we are concerned with a physiological peculiarity without phylogenetic significance, since the pollen-tube always can grow through the tissues of the style.

The relative primitiveness of the Polycarpicae was first maintained by HALLIER (^{23}) in a number of papers. ARBER and PARKIN take the same view and DIELS (^{23}) has brought forward evidence in its support. More recently S. HUTCHINSON (^{23}) concurs in the derivation of the Angiosperms from the Polycarpicae. Serological investigation leads to the same result.

The following characters of the Polycarpicae support this view; the spiral arrangement of the numerous floral members on an elongated or broadened (*Calycanthus*) floral axis; apocarpous carpels; actinomorphic flowers, from which zygomorphic forms may be derived. A sharp distinction between calyx and corolla may be wanting; the capacity of plastic transformation of stamens into staminodes or petals is present; woody plants still without vessels are met with. Entomophily, with Coleoptera as the floral visitors as in *Encephalartos*, is found in *Eupomatia* and *Calycanthus*.

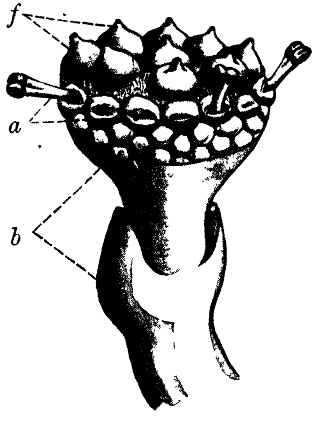


FIG. 636.—*Gnetum Gnemon.* *a*, stamens; *b*, bracts; *f*, carpels.

Just as WETTSTEIN attempted to derive the Verticillatae and Fagales, which he regards as the lowest Angiosperms, from *Ephedra*, on this alternative view the Polycarpicae are compared with *Gnetum* (cf. Fig. 632 and its explanation). That the Bennettitaceae do not come into the comparison as was the opinion of ARBER and PARKIN (^{23}) has already been pointed out by KARSTEN (^{23}), and THOMPSON (^{23}), though he is arguing for a derivation from the Amentiferae, comes to the same conclusion. The spiral arrangement of the ♂ flowers is seen in Fig. 636, which represents a male inflorescence of *Gnetum Gnemon*, consisting of only one whorl; above the circle of ♀ flowers (cf. Fig. 632) the structure ends, as was shown by STRASBURGER, with a terminal female flower. The presumably fertile female flowers have a perigone and two integuments, the inner of which projects and excretes a drop of fluid to catch the pollen: this fluid has a sweet taste and is eagerly sought by ants, etc. THOMPSON states that the pollen-grains frequently do not reach the tip of the nucellus but are retained in a dilatation of the micropylar tube; since they here germinate he regards this as a further approach to the relations found in an angiospermic flower. The decussate bracts are approximated to one another beneath the inflorescence. The main difficulties concern the male flowers, each of which has its perigone and an anther with two thecae; the origin of an anther with four thecae might come about by the development of a septum in each loculus. If the origin of an angiospermic flower from such a whorl of flowers is pictured, the bracts would necessarily be supposed to enlarge as the protective organs of the flower (calyx or perigone), and thus be closed together in the bud. The result of this would be that the individual perianths of the male flowers would no longer be necessary, and (on the analogy of the reduction of the seed-coat in a drupe, when the function of protection is taken over by the hard layer of the pericarp, cf. p. 592) would be gradually reduced and ultimately disappear. STRASBURGER has shown that the perianth of the female flowers may be regarded as an investment of the ovule, *i.e.* a carpel. In this way the condition of an entomophilous hermaphrodite flower with apocarpous carpels, such as is found in the Polycarpicae, could be attained.

It appears as if this line of derivation of the flower presents no greater difficulties than that of the Verticillatae from the inflorescence of *Ephedra*.

If the attempt is made to derive the various families from the Polycarpicae, the Monocotyledons (^{23a}), and in particular the Helobiae, can be connected directly to the Nympheaceae and Ranunculaceae by reason of their floral organisation, anatomical structure, and other characters. This is the usual assumption.

The arrangement would take the form represented in the scheme on p. 622. The Polycarpicae, according to HUTCHINSON (^{23}), are divided into the woody forms, the Magnoliales, and the more herbaceous series, the Ranales. The reduced series are here derived from the Magnoliales, passing by the Hamamelidales and Centrospermae back to the Fagales (Verticillatae). Returning then to the Ranales, an ascending line can be followed from the Rhoeadales to the Myrtales. The derivation from the Polycarpicae of the Euphorbiales is more questionable; from the latter group the Columniferae and the Gruinales can be derived, and they in turn lead to the main body of the Sympetalae.

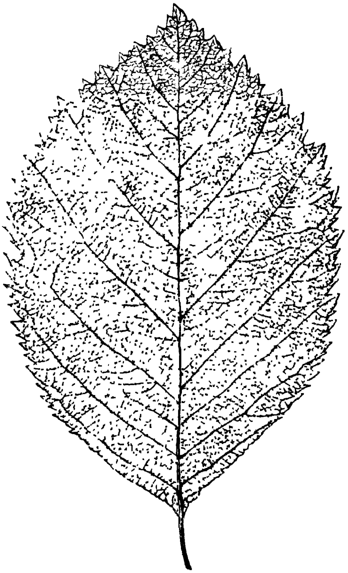


FIG. 637.—Leaf of *Crataegus* with reticulate venation. (⅔ nat. size. After NOLL.)

SUB-CLASS I

Dicotylae

The Dicotyledons with few exceptions possess a pair of seed-leaves. (Germination, cf. p. 80; stem and root, cf. p. 124.) They have secondary growth in thickness (cf. p. 133).

The typical form of leaf found among Dicotyledons is provided with a longer or shorter petiole, and often has a pair of stipules developed from the leaf-base; a leaf-sheath is usually absent (exception, Umbelliferae). The lamina may be simple or compound. The margin of the leaf presents considerable variety. The venation is as a rule reticulate (Fig. 637).

Series and Families of Angiosperms in their probable Phylogenetic Relations

Gymnospermae.	Dicotyledonae.	A. Choripetalae.	B. Sympetalae.	Monocotyledoneae.
	Reduced orders. ↑ **Magnoliales.** Magnoliaceae, Anonaceae, Myristicaceae. Calycanthaceae. Lauraceae. Aristolochiaceae.	**Verticillatae.** Casuarinaceae. **Fagales.** Betulaceae, Cupuliferae. **Juglandales.** Juglandaceae. **Salicales.** Salicaceae. **Urticales.** Ulmaceae, Moraceae, Cannabinaceae, Urticaceae. **Santalales.** Santalaceae, Loranthaceae, Balanophoracaceae. **Piperales** Piperaceae. **Polygonales.** Polygonaceae. **Centrospermae.** Caryophyllaceae, Chenopodiaceae, Aizoaaceae, Cactaceae. **Hamamelidales.** Hamamelidaceae, Platanaceae.	**Primulales.** Primulaceae.	
Gnetaceae (especially Gnetum, or similar Gymnosperms).	**Polycarpicae.** **Ranales.** Berberidaceae. Menispermaceae. Ranunculaceae Nymphaeaceae. ↓ Ascending orders.	**Rhoeadales.** Papaveraceae, Fumariaceae, Capparidaceae, Cruciferae. **Parietales.** (incl. Guttiferales). Cistaceae, Violaceae, Ternstroemiaceae (Theaceae), Dipterocarpaceae. **Rosales.** Crassulaceae, Saxifragaceae, Rosaceae. **Leguminosae.** Mimosaceae, Caesalpiniaceae, Papilionaceae. **Myrtales.** Thymelaeaceae, Elaeagnaceae, Lythraceae, Onagraceae, Rhizophoraceae, Myrtaceae, Punicaceae.	**Cucurbitaceae.** (Synandrae). **Bicornes.** Ericaceae.	**Monocotyledonae.** **Helobieae.** Alismataceae, Potomogetonaceae, Naiadaceae, Hydrocharitaceae. **Spadiciflorae.** Typhaceae, Sparganiaceae, Pandanaceae, Palmae, Araceae. **Liliiflorae.** Juncaceae, Liliaceae, Amaryllidaceae, Iridaceae. **Enantioblastae.** Commelinaceae. **Glumiflorae.** Cyperaceae, Gramineae. **Scitamineae.** Musaceae, Zingiberaceae, Cannaceae, Marantaceae. **Gynandrae.** Orchidaceae.
	Euphorbiales. Euphorbiaceae. Buxaceae.	**Columniferae.** Malvaceae, Tiliaceae, Sterculiaceae. **Gruinales.** Geraniaceae. Linaceae, Erythroxylaceae, Zygophyllaceae, Rutaceae, Simarubaceae, Burseraceae, Polygalaceae, Sapindaceae, Anacardiaceae, Aquifoliaceae, Aceraceae, Hippocastanaceae. **Rhamnales.** Rhamnaceae, Vitaceae.	**Diospyrales.** Ebenaceae, Sapotaceae, Styracaceae. **Contortae.** Oleaceae, Loganiaceae, Gentianaceae, Apocynaceae, Asclepiadaceae. **Tubiflorae.** Convolvulaceae, Borraginaceae, Verbenaceae, Labialae. **Personatae.** Solanaceae, Scrophulariaceae, Orobanchaceae, Lentibulariaceae, Plantaginaceae.	
		Umbelliferae.	**Rubiales.** Rubiaceae, Caprifoliaceae, Valerianaceae, Dipsaceae. **Synandrae.** Cucurbitaceae, Campanulaceae, Lobeliaceae, Compositae.	

The flowers in Dicotyledons are typically pentamerous and pentacyclic, but there are numerous exceptions to this. The floral formula in the most regularly constructed representatives is K5, C5, A5 + 5, G5.

A. Choripetalae

(Petals not coherent)

Order 1. Polycarpicae

Hermaphrodite, usually brightly coloured flowers, with an elongated receptacle on which the free perianth-segments, the stamens and the apocarpous carpels are spirally arranged; the carpels are indefinite in number and may be very numerous. The separation of calyx and corolla is frequently indistinct, and in some cases (*e.g. Calycanthus*) even the foliage-leaves pass with their spiral arrangement into the bracts of the flower. The stamens have frequently a leaf-like form with the connective continued beyond the anthers, or forming a leafy expansion. The stigma terminates the carpel without a definite style.

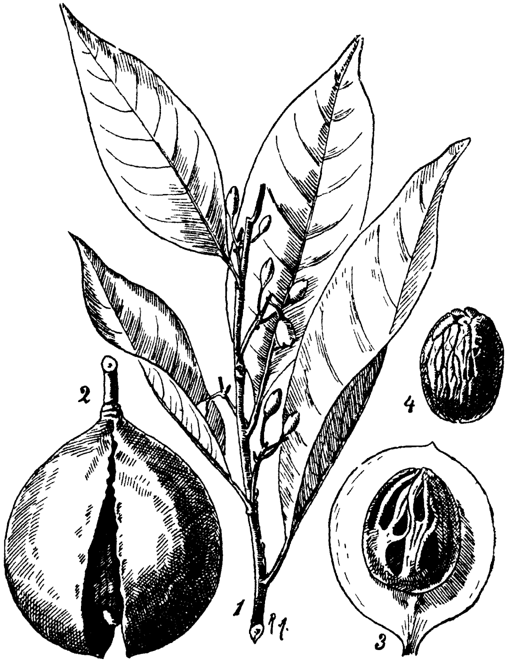


FIG. 638.—*Myristica fragrans*. *1*, Twig with male flowers (½ nat. size). *2*, Ripe pendulous fruit, opening. *3*, Fruit after removal of one-half of the pericarp, showing the dark brown seed surrounded by the ruptured arillus (Mace). *4*, Kernel freed from the seed-coat.

Pollination by means of insects (in some primitive forms by beetles) is general.

It is only possible to deal here with the most important forms.

The various families of Polycarpicae, although they frequently do not exhibit all the distinguishing characteristics, are phylogenetically connected ; this is serologically confirmed. They fall into two sub-orders which are distinguished by HUTCHINSON as the **Magnoliales** and **Ranales**. The Magnoliales are nearly all woody plants, the more simply constructed flowers of which (Myristicaceae, Calycanthaceae, Lauraceae, Aristolochiaceae) are less highly organised than the flowers of the Ranales ; in the latter they are usually brightly coloured and with a differentiation into calyx and corolla. The Magnoliales are further characterised by possessing cells with ethereal oils. Their lower position is indicated also by the primitive type of wood of some forms from which vessels are absent. (*Drimys* (23), cf. p. 143.)

Sub-Order 1. Magnoliales

Family 1. **Magnoliaceae.**—The plants of this family are all woody with large terminal flowers. The perianth-leaves, without distinction into sepals and petals, the numerous stamens, and the apocarpous carpels are all spirally arranged in ascending order on the elongated floral axis. The stigma terminates the carpel without intervening style. Oil-cells in the stem and leaves Pollen-grains with one germ-pore *Drimys* and *Zygogynum* have wood without vessels, like the Coniferae. *Magnolia* and *Liriodendron* (Tulip tree) are frequently cultivated

OFFICIAL —Star-anise, obtained from *Illicium verum*, yields OLEUM ANISI. The fruits of *Illicium religiosum* (Japan) are poisonous.

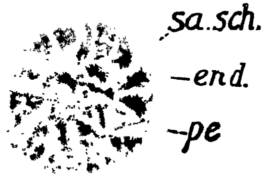


FIG. 639.—*Myristica* Transverse section of seed *sa sch*, Seed coat; *end*, endosperm, *pe*, perisperm

Family 2 **Anonaceae.**—Woody plants of the tropics, with spirally arranged stamens and apocarpous gynaeceum ; seeds with ruminated endosperm.

Family 3. **Myristicaceae.**—Resembles the preceding family, but the dioecious flowers are more simply constructed (Figs 638, 639).

OFFICIAL.—MYRISTICA, Nutmeg. The seed of *Myristica fragrans* divested of its testa yields OLEUM MYRISTICAE.

Family 4. **Calycanthaceae** —These plants show a continuous sequence from the foliage leaves to the numerous free perianth-leaves, stamens, and carpels borne on the depressed floral axis.

Family 5. **Lauraceae.**—Flower also composed of trimerous whorls ; perianth 3+3 ; stamens 3+3. The three stigmas of the single, one-seeded pistil indicate its origin from three coherent carpels. Fruit, a berry or drupe. Anthers valvate. Aromatic trees or shrubs with entire leathery leaves, which usually persist for several seasons. Only *Sassafras* (Fig. 643), which has three-lobed leaves as well as simple ones, sheds its foliage annually. *Laurus nobilis*, the Laurel, is a dioecious, evergreen tree of the Mediterranean region (Figs. 640, 641). Large plantations are grown at the Lake of Garda, where the oil is extracted, and here the trees ripen their oval, blackish-blue drupes in October. The genus *Cinnamomum* includes a number of economically important trees such as the Camphor

FIG. 640.—*Laurus nobilis* with male flowers. (½ nat. size.)

FIG. 641.—*Laurus nobilis* with fruits. (½ nat. size.)

tree from Japan and China and the Cinnamon tree from China and Ceylon. The latter is a stately evergreen with smooth, leathery leaves and inconspicuous, greenish flowers in axillary inflorescences. *Persea gratissima* (Fig. 642) is a native of tropical Mexico, and is frequently cultivated as a fruit tree in the tropics. Its fruit is known as the Avocado Pear. Species of *Cassytha*, the only genus of the family including herbaceous species, occur throughout the tropics as parasites resembling *Cuscuta.*

OFFICIAL.—CAMPHORA, Camphor, is obtained from *Cinnamomum Camphora.* CINNAMOMI CORTEX and OLEUM CINNAMOMI from *Cinnamomum Zeylanicum. Cinnamomum Oliveri* yields OLIVERI CORTEX.

Family 6. **Aristolochiaceae.**—The zygomorphic flowers (Fig. 568) have a simple coherent perianth and the androecium and gynaeceum united to form a gynostemium. OFFICIAL.—*Aristolochia serpentaria, A. reticulata* yield SERPENTARIAE RHIZOMA.

The parasitic **Rafflesiaceae** ([24]) and the insectivorous families of the **Cephalotaceae, Sarraceniaceae,** and **Nepenthaceae** may best be placed with the Aristolochiaceae in the Polycarpicae.

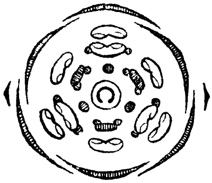


FIG. 642.—Floral diagram of *Persea* (After EICHLER.)

Order 2. Hamamelidales ([25])

This includes the two Families **Hamamelidaceae** and **Platanaceae.**—Woody plants, with stipulate leaves. Flowers as a rule inconspicuous, without perianth and anemophilous. Conspicuous, entomophilous flowers with a simple or, more rarely, double perianth also occur. Two carpels.

OFFICIAL.—STYRAX PRAEPARATUS from *Liquidambar orientalis.* HAMAMELIDIS CORTEX and FOLIA from *Hamamelis virginiana.*

Platanus orientalis and *P. occidentalis* are commonly planted as shade-trees by the sides of streets.

On the affinities of this order see HALLIER ([25]) who regard these plants as an important connecting link between the Gymnosperms and the Polycarpicae.

Order 3. Centrospermae

Herbaceous plants with as a rule hermaphrodite flowers which have a perianth of two whorls, the corolla being coloured. The campylotropous ovules and as a rule the free-central placentation are characteristic. This agrees with the connection with the Primulales which is indicated serologically.

Family 1. **Caryophyllaceae.**—Herbs, with simple, linear, usually opposite leaves; flowers typically pentamerous, with calyx and corolla. Two whorls of stamens, obdiplostemonous Unilocular or incompletely septate ovary. K 5, C 5, A 5 + 5, G $\underline{(5)}$ (Fig. 645). Fruit, a capsule. Seeds numerous, embryo curved around the floury perisperm. The number of carpels ranges from 2 to 5.

Cerastium and *Stellaria* have white flowers and bifid petals, and are conspicuous, early-flowering forms. Species of *Dianthus*, Pinks, have frequently attractive colours and scent, and occur in dry, sunny situations. *Agrostemma Githago* (Fig. 646), Corn-cockle, is a hairy plant with pink flowers. It is a common weed in corn-fields : its seeds are poisonous. *Saponaria officinalis* is a herb attaining the height of a metre, with opposite, broad leaves and rose-coloured flowers. The saponin contained in all parts of the plant renders it poisonous (Fig. 644).

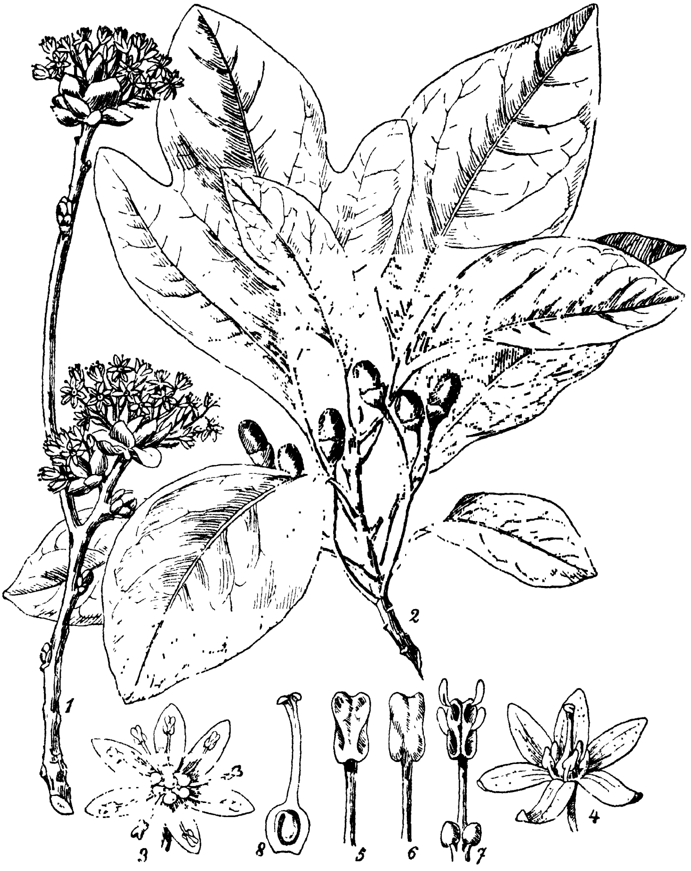


Fig. 643.—*Sassafras officinale.* (½ nat. size. After Berg and Schmidt.) *1*, Male inflorescences on a still leafless branch. *2*, Fruits on a leafy shoot. *3*, Male flower. *4*, Female flower. *5*, *6*, Closed stamens of the two outer whorls. *7*, Opened stamen of the innermost whorl. *8*, Ovary showing the style and the ovule.

Family 2. **Chenopodiaceae.**—Herbs, rarely small woody plants, with alternate leaves. Flowers typically pentamerous, with a single whorl in both perigone and androecium; P 5, A 5, $G\ \underline{(2\text{-}5)}$. Stamens opposite the perianth-leaves. Reduced, unisexual flowers are not infrequent. The unilocular ovary contains a basal, campylotropous ovule. Fruit, a nut. Seed with a curved embryo.

This family exhibits reduction in its usually colourless perianth.

Many of the Chenopodiaceae are strand-plants (*Salicornia*, cf. p. 164, Fig. 188), or occur on soils containing a large amount of salt, such as the great Asiatic salt steppes and deserts. The Spinach (*Spinacia oleracea*) and the Summer Spinach (*S. glabra*) are used as vegetables. The Sugar Beet (*Beta vulgaris*, var. *rapa*) is a plant of great economic importance. It is a biennial plant, and in the first season forms a thick, swollen root bearing a bud consisting of a number of thick-stalked, entire, succulent, and often crisped leaves. From this rosette of leaves there springs in the second season a highly branched panicle, bearing the inconspicuous greenish flowers. Ovary formed of three carpels. At the end of the first season the root contains cane-sugar as a reserve-material, which at this stage is extracted from the plant. By constant selection the percentage of sugar is raised from 7-8 % to an average of 15 %. The original form of the Sugar Beet is *Beta patula*. *Chenopodium* and *Atriplex* are common weeds near human dwellings.

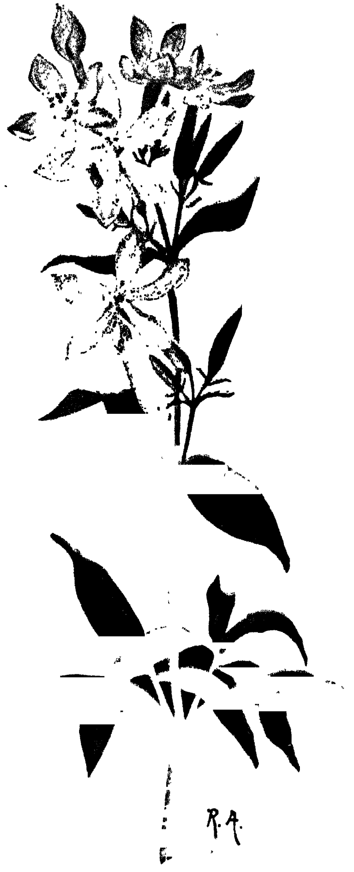


FIG. 644.—*Saponaria officinalis* (½ nat. size). POISONOUS.

The two following families are greatly reduced as an adaptation to adverse conditions of life.

Family 3. **Aizoaceae.**—*Mesembryanthemum*; perennial herbaceous xeromorphic plants with succulent leaves. Flowers hermaphrodite; with a polypetalous corolla derived from modified stamens. Stamens numerous. Carpels 2-∞; united to form the hygroscopic capsule. South African. The genus includes plants which "mimic" pebbles, *e.g. Mesembryanthemum truncatellum*, *M. pseudo-truncatellum*, *M. Bolusii*, *M. calcareum*, etc. (26).

Family 4. **Cactaceae.**—For the most part leafless plants with succulent stems, natives of America. In size they range from very small to gigantic forms. Flowers

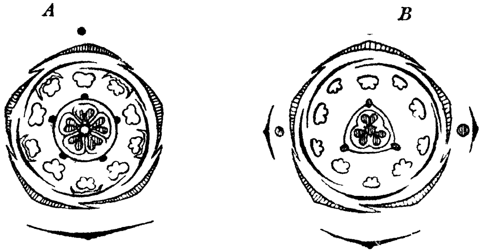


FIG 645 — Diagrams of the Caryophyllaceae A *Viscaria* septa present in the lower part of the ovary B *Silene* septa absent (After EICHLER)

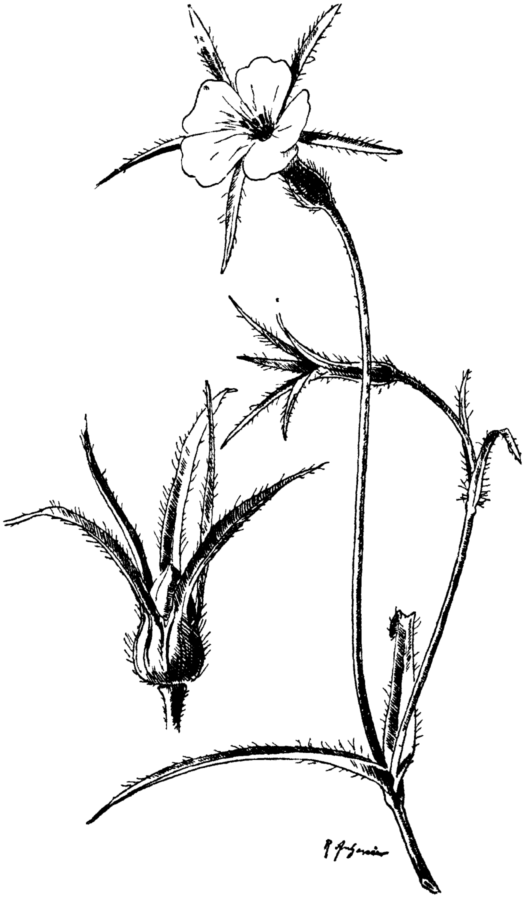


FIG 646 —*Agrostemma Githago* Flowering shoot and fruit (½ nat size). ***POISONOUS***

hermaphrodite, actinomorphic, less commonly dorsiventral. Perianth of many members, spirally arranged and showing a gradual transition from the calyx to the corolla. Stamens and carpels numerous. Ovary inferior, unilocular, with numerous parietal placentas. Ovules with long stalks. Fruit, a berry, the succulent tissue being largely derived from the stalks of the seeds. Closely related by floral structure and anatomy to the Aizoaceae.

Only *Peireskia* and some species of *Opuntia* possess leaves. Other species of *Opuntia* have flattened branches (Fig. 190). *Cereus* (Fig. 194), *Echinocactus*, etc., with longitudinal ridges on the stem ; *Mamillaria* has free projections (mamillae). The numerous groups of spines on the shoots, ribs, or separate mamillae correspond to axillary shoots, the subtending leaves of which are reduced, while the leaves of the expanded axis of the axillary shoot are metamorphosed into spines (Fig. 647).

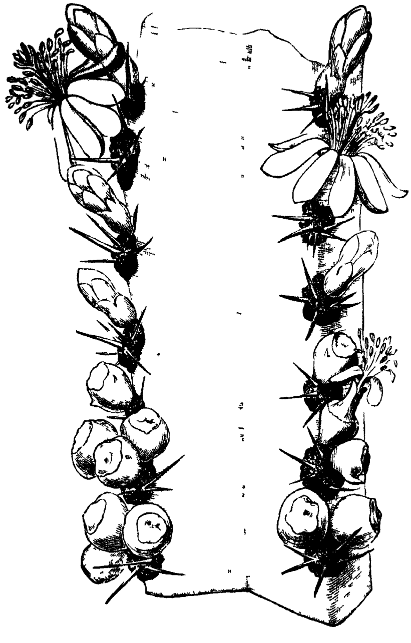


FIG. 647.—*Cereus geometrizans*. Two of the ribs or ridges of a five ribbed stem bearing flowers and fruits ($\frac{3}{4}$ nat. size).

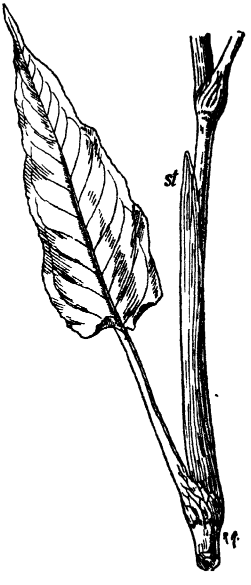


FIG. 648.—Leaf of *Polygonum amplexicaule* showing the ochrea, *st* ($\frac{1}{3}$ nat. size).

Cactaceae form a dominant constituent of the vegetation in the dry south-western regions of the United States, in Mexico, and in the Andes of South America. A similar habit is found in some Euphorbiaceae and Asclepiadaceae living under corresponding climatic conditions (cf. p. 165 Convergence). There are numerous epiphytic Cactaceae, especially species of *Rhipsalis*, *Epiphyllum*, and *Phyllocactus*. *Opuntia ficus indica* has become naturalised in the Mediterranean region. The fruits of this species and of others of the genus are edible, and the plants are

Order 4. Polygonales (27)

Family 1. **Polygonaceae.**—For the most part perennial herbs, with hollow stems swollen at the nodes, and alternate, simple leaves. The membranous stipules of the latter are coherent to form a sheath or OCHREA protecting the terminal bud ; when broken through by the growth of the stem, this remains as a tubular sheath around the lower part of the internode (Fig. 648). Perianth simple, usually colourless ; ovules atropous.

Mainly natives of the North Temperate zone.

GENERA.—*Rheum*, Rhubarb. This is an East Asiatic genus, originating from the mountains of China, with large, radical leaves and a large, spreading, paniculate inflorescence. Leaves simple, cordate-reniform, with palmate venation, sometimes more or less lobed. The flower has a perigone of two similar whorls, and two whorls of stamens, the outer whorl being double by chorisis ; P 3 + 3, A 6 + 3, G $\underline{(3)}$. Nectar for visiting insects is secreted by the large scales of the disc. The triangular ovary becomes winged as it develops into the fruit (Fig. 649 *D*). Species of *Rheum* are cultivated as ornamental plants and as vegetables. *Rumex acetosa*, Sorrel, with sagittate leaves. The structure of the flowers of the hermaphrodite species of *Rumex* is similar to that of *Rheum*, but the inner whorl of stamens is wanting. On parthenogenesis in *Rumex*, cf. ROTH (27). The species of *Polygonum* have a perigone consisting of five coloured leaves and a varying number of stamens. The triangular fruits of *Fagopyrum esculentum* form Buckwheat (Fig. 608 *B*).

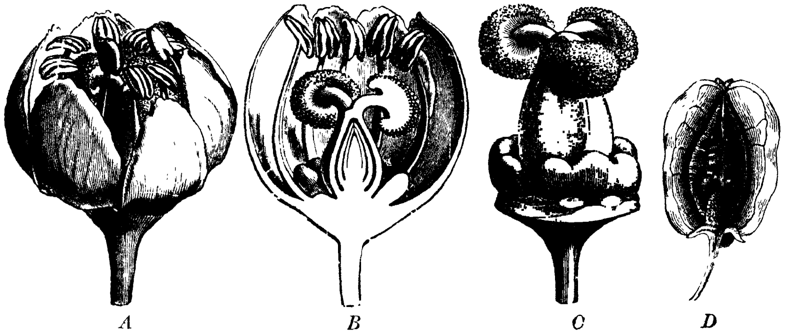


FIG. 649.—*Rheum officinale.* *A*, Flower ; *B*, the same cut through longitudinally ; *C*, gynaeceum with disc. *Rheum compactum* : *D*, fruit. (After LÜRSSEN, magnified.)

OFFICIAL.—*Rheum officinale*, *Rh. palmatum*, and probably other species yield RHEI RHIZOMA.

Order 5. Piperales

Single Family. **Piperaceae.**—The genus *Piper* is important. Flowers as a rule unisexual and without perianth, associated in spikes; typically trimerous but usually reduced. Ovary unilocular, ovule solitary, basal and atropous. Fruit drupe-like. The embryo is embedded in a small endosperm surrounded by a well-developed perisperm. The vascular bundles are scattered in the cross-section of the stem resembling the arrangement in Monocotyledons, but with secondary thickening.

Piper nigrum, from which the Peppers are derived, is the most important representative. This is a root-climber, native to the Malayan region, but now cultivated throughout the tropics (Fig. 650). The unripe fruits provide black pepper, while white pepper is obtained from the ripe fruits after removal of the outer layers of the pericarp. *Peperomia* (28), tropical shade-plants and epiphytes.

OFFICIAL.—*Piper cubeba* (Fig. 651) is a native of Java and is distinguished by the stalk-like base of the fruit from that of the Black Pepper. It provides CUBEBAE FRUCTUS, OLEUM CUBEBAE, TINCTURA CUBEBAE. *Piper Betle* yields BETEL. *Piper methysticum* yields KAVAE RHIZOMA.

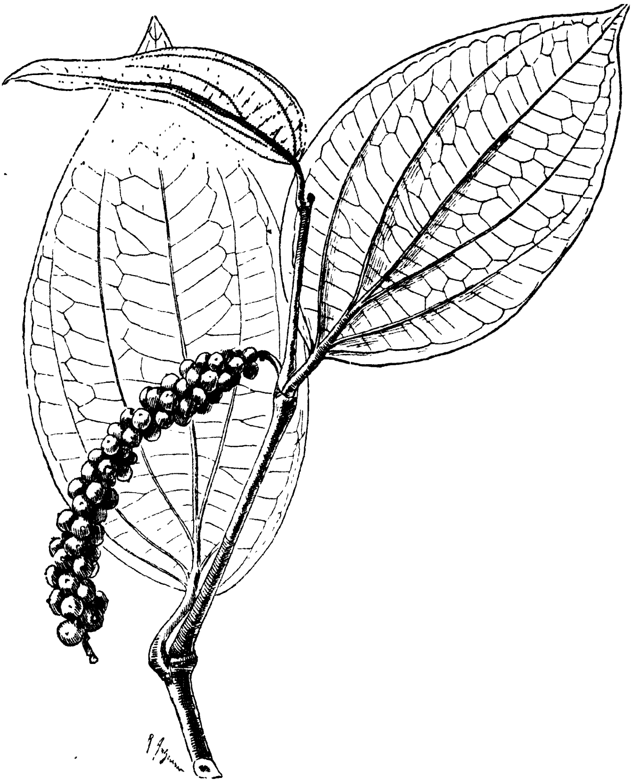


FIG. 650.—*Piper nigrum.* (½ nat. size.)

Order 6. Santalales (29)

Family 1. **Santalaceae.**—Green plants growing in the soil and partially parasitic on the roots of other plants from which their haustoria obtain nutrient materials. In Britain, *Thesium.*

OFFICIAL.—*Santalum album,* the wood of which when distilled yields OLEUM SANTALI.

Family 2. **Loranthaceae.**—Leafy semi-parasitic shrubs, living on the branches of trees. They are most abundant in the tropics, and, for instance in South America, add to the beauty of the forest by their brightly coloured, ornithophilous flowers.

Loranthus europaeus, on Oaks in Europe. In Britain *Viscum album* (Fig. 652), the Mistletoe, occurs as an evergreen parasite on a number of trees. It has opposite, obovate leaves. Stem swollen at the nodes. The white berries are distributed by birds. The sucker, without a root-cap, emerging from the seed penetrates the cortex of the host to the wood, into which it cannot grow. Its tip becomes embedded in the new wood formed by the cambium of the host. Further growth in length of the sucker is effected by a zone corresponding in position to the cambium of the host. Reduction in relation to parasitism is seen in all the genera and species.

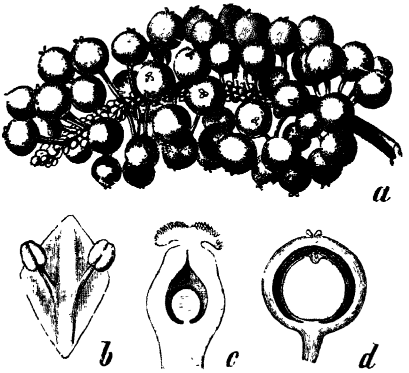


FIG. 651.—*Piper cubeba*. *a*, Infructescence; *b*, a male flower; *c*, a female flower in longitudinal section; *d*, fruit in longitudinal section. (After BERG and SCHMIDT.)

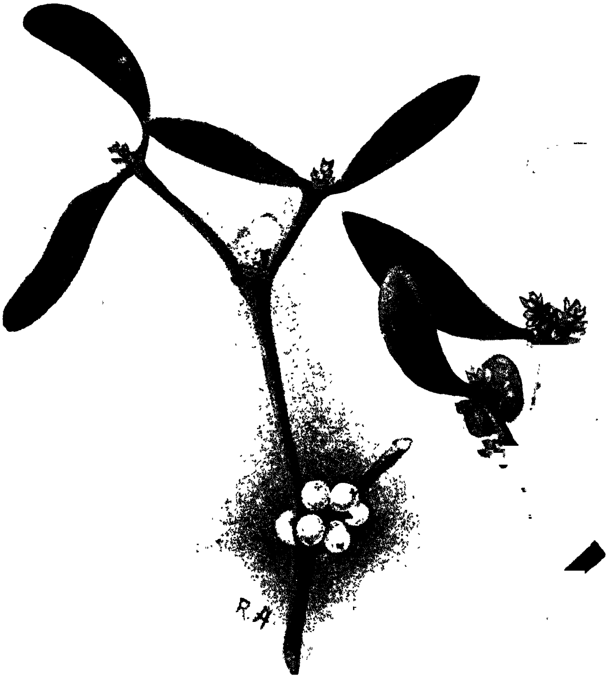


FIG. 652.—*Viscum album*. With flowers and fruits. (½ nat. size.)

Order 7. Urticales

Plants with usually diclinous small flowers closely aggregated in the inflorescence. Stamens equal in number to the leaves of the perigone and superposed on the latter. Ovary superior, composed of one or two carpels, usually unilocular, and containing a single, pendulous ovule. Fruit, a nut or drupe. Seeds usually containing endosperm.

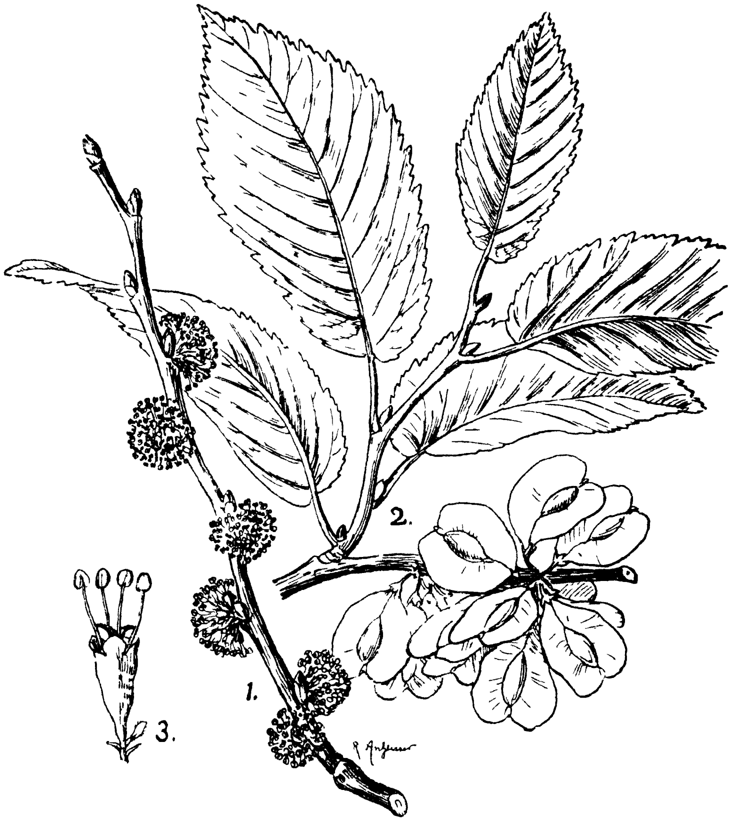


FIG. 653.—*Ulmus campestris* ($\frac{1}{3}$ nat. size). *1*, Branch with flowers. *2*, Branch with fruits. *3*, Single flower enlarged.

Family 1. **Ulmaceae.**—*Ulmus campestris* (Fig. 653), the Elm, is a common European tree. The arrangement of the leaves on the sides of the twigs in two rows and the corresponding branching leads to the leaf-surface exposed on each lateral branch making a definite angle with the main branch and composing the regular convex crown of foliage exhibited by older examples. The leaves are always asymmetrical. The flowers stand in groups in the axils of the leaves of the previous year; they are hermaphrodite or, by abortion, unisexual. The stamens are straight in the bud. The tree flowers in February or March, and the fruits ripen before the leaves expand. The fruits are broadly winged and adapted to be carried by the wind. *U. montana*, *U. effusa* are closely related forms. Several species of *Celtis*, in which the fruit is a drupe, are in cultivation.

Family 2. **Moraceae.**—The majority are trees or shrubs with abundant latex. Leaves alternate, stipules caducous. Flowers unisexual, in globular or disc-shaped inflorescences; mostly tetramerous.

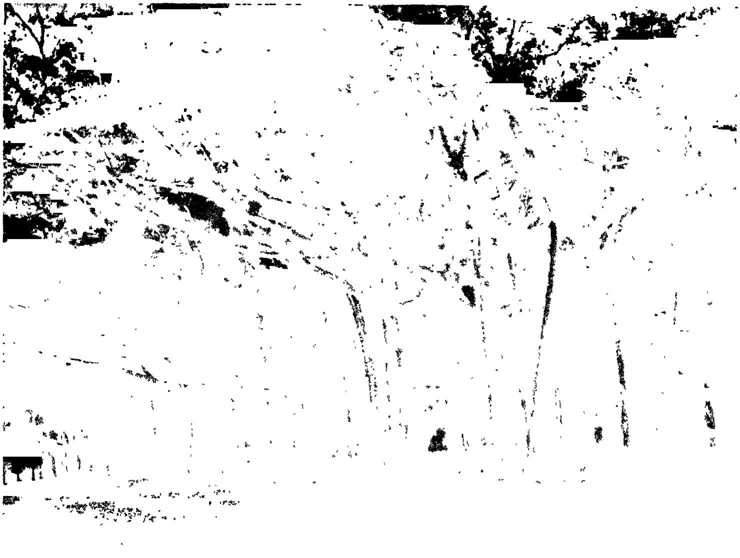


FIG. 654.—*Ficus bengalensis* in the Botanic Garden at Buitenzorg.

IMPORTANT REPRESENTATIVES.—In addition to the Mulberry trees, of which *Morus alba* is cultivated for the rearing of Silk-worms and *M. nigra* (Fig. 611 *B*) as a fruit-tree, the genus *Ficus* deserves special mention. The species occurring farthest north is the Common Fig (30) (*Ficus carica*, Fig. 563), which is endemic to the Mediterranean region, and has been long cultivated. It is a low tree with palmately incised leaves and stipules, which form a cap-like protection to the bud. The inflorescences are hollow, pitcher-shaped structures with a narrow opening. The flowers are borne closely crowded together on the inner surface. The flat, disc-shaped inflorescences of *Dorstenia* which bear the flowers on the upper surface are in many respects corresponding structures. On the distribution of the fruitlets cf. GOEBEL (31). On the pollination of the Fig cf. p. 568, Fig. 563. The sweet, fleshy portion of the edible Fig is developed from the hollowed axis of the inflorescence together with the perigones of the individual flowers. The small, hard, seed-like bodies are the fruits developed from the ovaries of the small flowers. Some species of *Ficus* are among the largest trees of tropical forests. The most remarkable is the Banyan (*Ficus bengalensis*), which occurs in the East Indies. The seeds, carried by fruit-eating birds, germinate on the branches of trees, where the plant develops as an epiphyte. The proper form of the tree is only seen, however, after the roots have reached the soil, and it is no longer dependent on the scanty food-supply obtainable in the epiphytic position. The host-plant is gradually strangled, additional roots are sent down to the soil and thicken into pillar-like supports, and ultimately a small wood capable of sheltering an entire village is developed from the single small seedling (Fig. 654). The latex of *Ficus* *elastica* is obtained from the tree by making incisions in the bark, and serves as one source of india-rubber. *Castilloa elastica* is another important rubber-tree of Central America. The gigantic inflorescences of species of *Artocarpus* when in fruit are eaten raw or cooked, and form the Bread-fruit of the tropics.

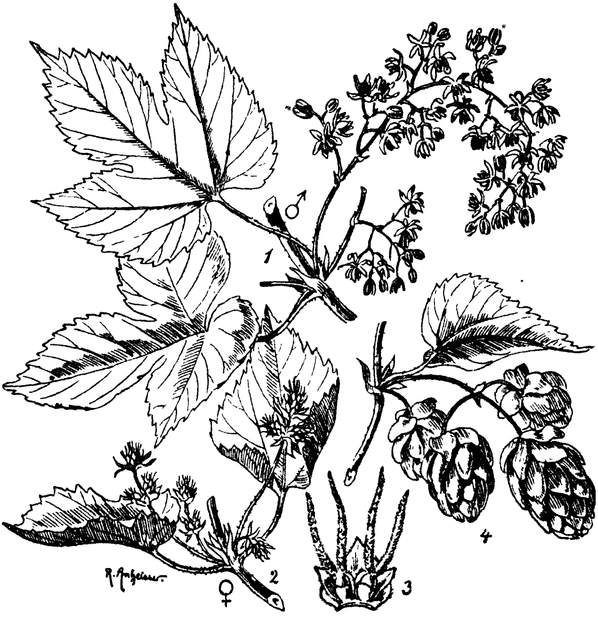


FIG. 655.—*Humulus lupulus*. *1*. Male inflorescence. *2*, Female inflorescence. *3*, Two female flowers in the axil of a bract. *4*, Cone-like inflorescences in fruit. (½ nat. size.)

Family 3. **Cannabinaceae.**—*Humulus lupulus*, the Hop (^{32a}), is a native of Central Europe; it has a perennial rhizome, which annually produces a crop of twining shoots (Fig. 655). The stem and opposite leaves bear coarse hairs, and the former bears hooked prickles which prevent it slipping down the support. The male flowers of this dioecious plant are pentamerous, with straight stamens and grouped in dichasia, the central branches of which are capable of further growth. The branches of the female inflorescence are catkin-like, the scales being formed of the pairs of stipules belonging to bracts, the laminae of which are suppressed. The axillary shoot of the bract is also suppressed, but each stipule has two flowers in its axil ; each flower is enclosed by its own bract. These bracts project beyond the stipules when the inflorescence is mature, and give the latter its cone-like appearance. Upon them are developed the glandular hairs on account of which the Hop is cultivated.

Cannabis sativa, Indian Hemp, is an annual herb with palmately divided, hairy leaves. The plant is utilised in Europe for its bast fibres, which are from one to several centimetres long. The glandular hairs which cover all parts of the female inflorescence secrete a sticky resinous substance which is used medicinally. In the East it is used in the preparation of a narcotic called Hashish.

OFFICIAL — *Cannabis sativa* provides CANNABIS INDICA.

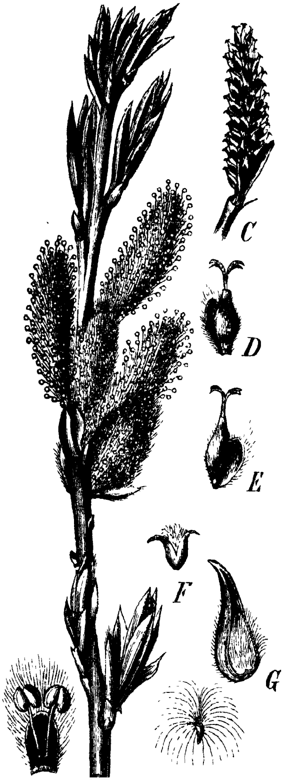


FIG. 656.—*Salix viminalis*. *A*, Flowering male twig (nat. size). *B*, Male flower with subtending bract (magnified). *C*, Female inflorescence. *D*-*E*, Female flowers (magnified). *F*, Fruit (nat. size). *G*, The same magnified. *H*, Seed (magnified). (After SCHIMPER.)

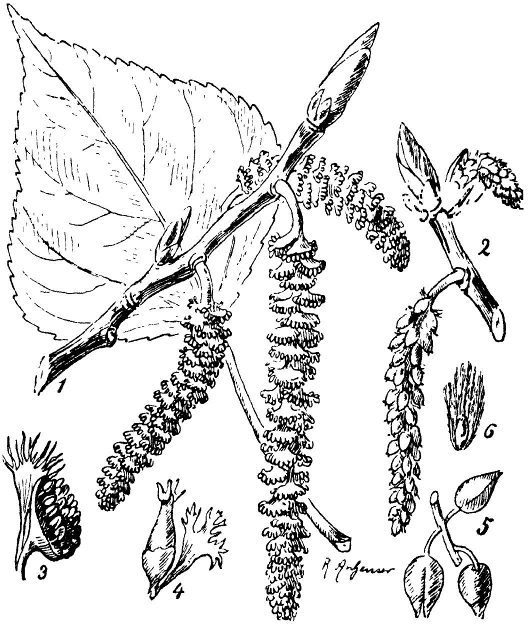


FIG. 657.—*Populus nigra*. *1*, Male inflorescence. *2*, Female inflorescence. *3*, Male flower. *4*, Female flower. *5*, Fruit. *6*, Seed. (*1*, *2*, ¾ nat. size ; *3-6*, enlarged.)

Family 4. **Urticaceae.**—Perennial herbs. Leaves simple, stipulate. Flowers unisexual by suppression of parts, as a rule bimerous. P 2 + 2, A 2 + 2. Stamens inflexed in the bud, and scattering the pollen when they suddenly straighten. Perianth of the female flower adherent. Ovary consisting of a single carpel, unilocular, with a basal, atropous ovule. The ripe fruits of species of *Pilea* and *Elatostemma* are forcibly dispersed by means of organs developed from staminodes (^{31}).

A number of the Urticaceae are characterised by the possession of stinging hairs (cf. Fig. 49). Some provide important fibres, especially *Boehmeria nivea* from which Ramie fibre is obtained. Our native species of *Urtica* provided textile fibres in the times before cotton was discovered, and were again employed during the war.

Order 8. Salicales

Family **Salicaceae.**—Dioecious trees and shrubs with simple, alternate, stipulate leaves. Flowers in catkins greatly reduced. Ovary of two carpels, unilocular. Fruit, a capsule containing numerous, parietal seeds. Seeds without endosperm.

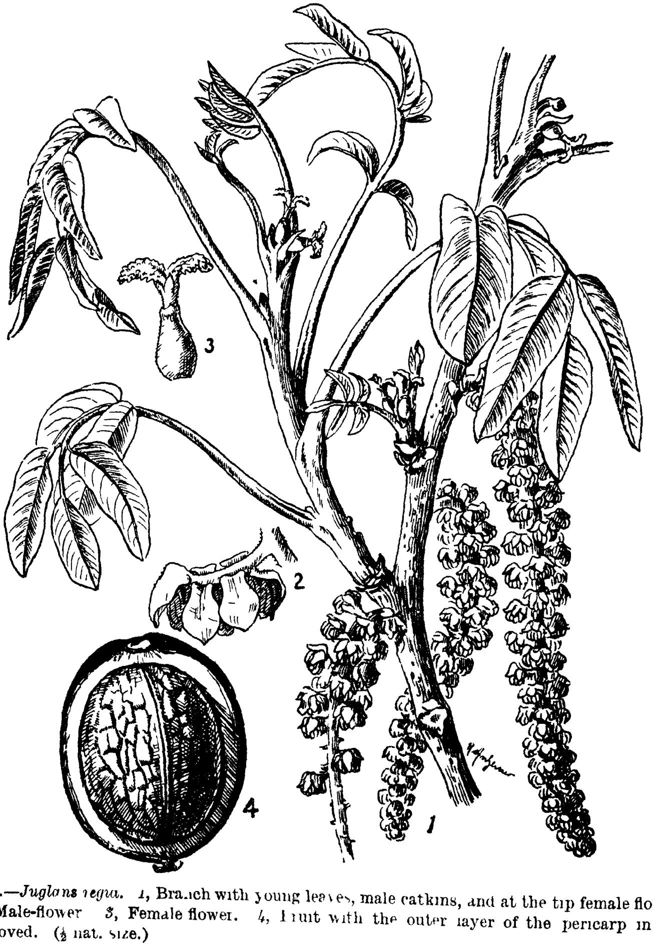


FIG. 658.—*Juglans regia.* *1*, Branch with young leaves, male catkins, and at the tip female flowers. *2*, Male-flower *3*, Female flower. *4*, Fruit with the outer layer of the pericarp in part removed. (½ nat. size.)

This family is mainly represented in the north temperate zone. *Salix*, Willow, and *Populus*, Poplar, are the only genera. *Salix* has erect catkins and is adapted for pollination by insects; in relation to this, nectar is secreted by small scales at the base of the flower. Male flowers scented; pollen sticky. The number of stamens varies from two to five in the different species. Bracts entire (Fig. 656). Willows occur commonly by the banks of streams. Some species are among the more abundant plants of high northern latitudes; they have subterranean, creeping stems, only the young shoots projecting from the soil. *Populus* has anemophilous flowers; disc cup-shaped; no secretion of nectar. The long-stalked, roundish leaves of the Poplars give them a different habit from the Willows. Flowers similar to those of *Salix*, but with divided bracts. Catkins pendulous (Fig. 657).

OFFICIAL.—SALICINUM is obtained from the bark of species of *Salix* and *Populus*.

Order 9. Juglandales

Family **Juglandaceae.**—Conspicuous, monoecious trees of the northern hemisphere with imparipinnate, aromatic leaves arranged alternately. Stipules wanting. The reduced anemophilous flowers are grouped in catkins.

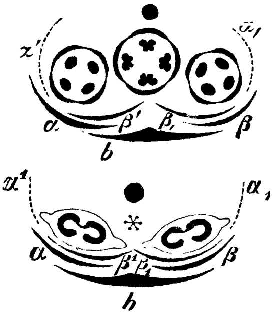


FIG. 659.—*Alnus glutinosa.* Diagrams of the male and female flowers. Bract *b*; bracteoles *a β*, *a′ β′*, *a, β,*. (After EICHLER.)

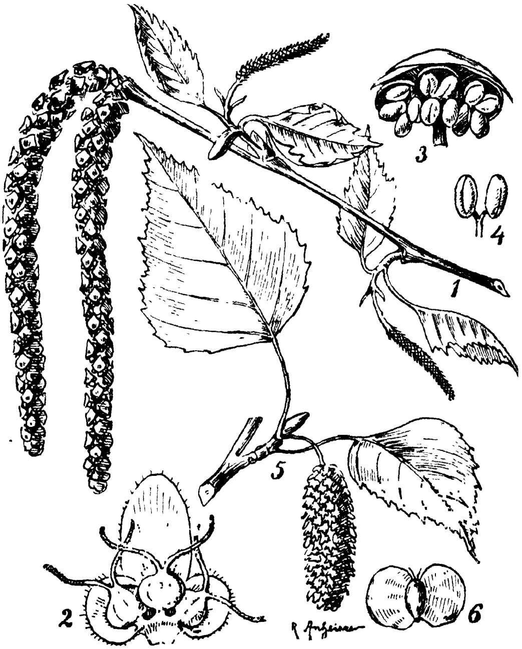


FIG. 660.—*Betula verrucosa.* *1*, Branch with terminal male catkins and female catkins on small lateral branches. *2*, Female flower. *3*, Male flower. *4*, Stamen. *5*, A catkin in fruit. *6*, Fruit. (*1* and *5*, ⅔ nat. size; *2-4* and *6*, enlarged.)

The Walnut, *Juglans regia* (Fig. 658), is the best-known representative of the family. It is endemic in Western Asia, but the tree is in cultivation throughout Europe. In spring the axillary buds of the previous season produce long, thick, pendulous ♂ catkins bearing numerous flowers. Each of the latter has 3-5 perianth-segments, and these, together with the two bracteoles, are adherent to the bract and surround the numerous stamens. The female flowers in smaller numbers are borne at the summit of the young shoots. The two carpels terminate in large, feathery, diverging stigmas. The perigone is adherent to the bract and bracteoles. The single loculus of the inferior ovary encloses an atropous, basal ovule. Fruit, a drupe, developed after chalazogamous fertilisation (NAWASCHIN) (15). The exocarp contains abundant tannin. Within the stone is the embryo, enclosed in a thin seed-coat. The large cotyledons, which contain oil, are lobed in correspondence with the false septa that project from the inner surface of the ovary. Endosperm wanting. Other species of *Juglans* and *Carya* yield edible seeds and valuable timbers.

Order 10. Fagales ([33])

Trees or shrubs usually with entire leaves and deciduous stipules.

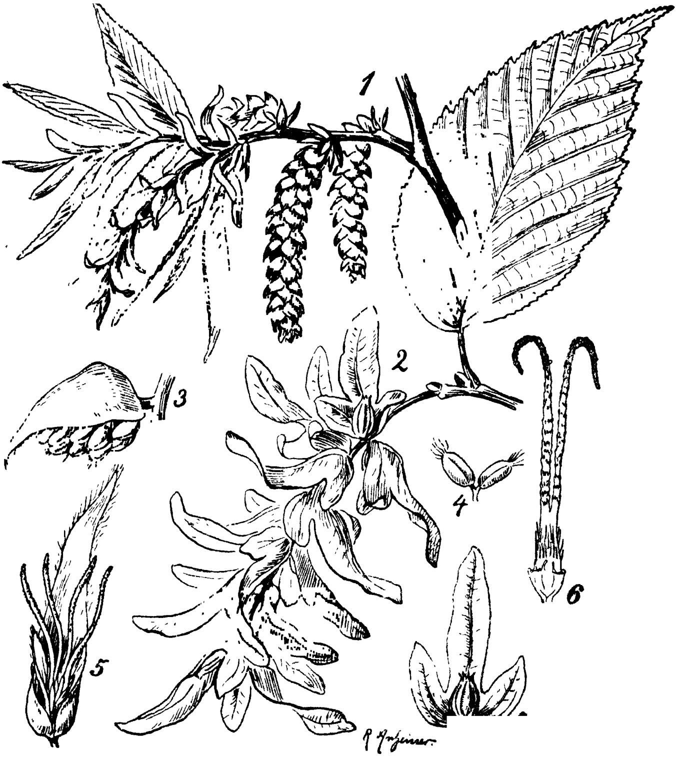


FIG. 661.—*Carpinus betulus.* *1*, Branch with male catkins projecting from the buds of the preceding year and female catkins on the growth of the current year. *2*, Female catkin in fruit. *3*, Male flower. *4*, Stamen. *5*, Bract with two female flowers. *6*, Female flower. *7*, Fruit. (*1*, *2*. *7*. $\frac{2}{3}$ nat. size; *3-6* enlarged.)

Monoecious. Flowers greatly reduced, anemophilous, in catkins. Ovary inferior; ovules pendulous, frequently chalazogamic. Fruit, a one-seeded nut. Endosperm wanting. This order includes most of our important forest-trees.

Family 1. **Betulaceae.**—Male flowers adherent to the bracts. Ovary bilocular, with two long stigmas; a single, pendulous ovule in each loculus. Mainly distributed in the northern hemisphere.

MOST IMPORTANT GENERA.—*Alnus glutinosa*, the Alder, is a prominent tree of damp woods, and is also distributed in swamps and by the banks of streams.

The inflorescences are already evident in the autumn as stalked catkins, the male long and pendulous, the female erect and short. Male flowers P4, A4 ; a dichasium of three flowers adherent to each bract (Figs. 560, 659). The female flowers are in pairs, their bracteoles adhering to the bract to form the five-lobed, persistent, woody scale of the cone. *Alnus incana* is distinguished by its leaves being grey and hairy below. The Alder has root-tubercles caused by bacteria which in symbiosis with their host-plant can assimilate free nitrogen. *Betula verrucosa* (Fig. 660), the Birch, has a white bark and long-stalked, triangular leaves. When young, all the parts are covered with numerous glandular hairs which give the plant an aromatic, resinous odour. The male inflorescences are formed in the autumn of the previous year, singly or a few together, at the tip of shoots of unlimited growth. Flowers P2, A2 ; in dichasia of three, adherent to the bract. Anthers deeply bifid (Fig. 660, 3, 4). Female inflorescences solitary, at the apex of small, short shoots of the current year. Flowers in dichasia of three in relation to each three-lobed scale ; the latter is composed of the bract and the two adherent bracteoles. Fruits borne on pendulous catkins ; winged. After the fruits are shed the scales of the catkin separate. *Carpinus betulus*, the Hornbeam (Fig. 661), is an important forest-tree. The inflorescences appear in spring ; the male, from axillary buds of the previous year, either want leaves or are accompanied by one or two, the female are usually terminal. The bract of the male catkin bears 4-10 stamens, bifid to the base, but without bracteoles or perigone. Two female flowers in relation to each bract ; each flower with its special bract and pair of bracteoles. The three later unite to form a three-lobed involucre which serves as an aid to distribution of the fruit by the wind. *Corylus avellana*, the Hazel, develops its inflorescences in the preceding year. The male catkins are freely exposed during the winter, while the female remain enclosed by the bud-scales, and only protrude their long red stigmas between the scales at the actual time of flowering. The male flower has no perianth but has a pair of bracteoles which are adherent to the bract, as are the four deeply bifid stamens. In the short female catkins a two-flowered dichasium is present in the axil of each bract as in *Carpinus* ; the fringed involucre also is derived from the coherent bracteoles and special bract of each flower. *Corylus tubulosa* from southern Europe.

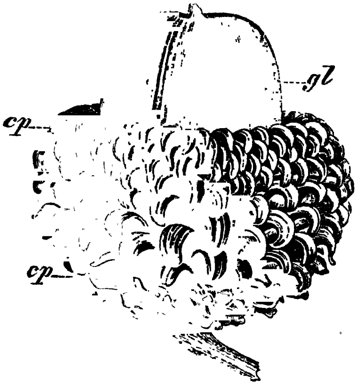


FIG. 662.—*Quercus Aegilops*. *cp*, cupula ; *gl*, fruit. (After DUCHARTRE.)

Family 2. **Cupuliferae.**—Inflorescences in the leaf-axils, bearing male flowers provided with a perianth, and female flowers, one or more of which are enclosed in a cupule (Fig. 664 *cp*) ; this in *Fagus* and *Castanea* is formed of coherent bracteoles, while the cupule of

Quercus arises as an annular growth from the axis (PRANTL-TROLL) (33)

Distributed chiefly in the temperate zones of the northern hemisphere, also in tropical Asia

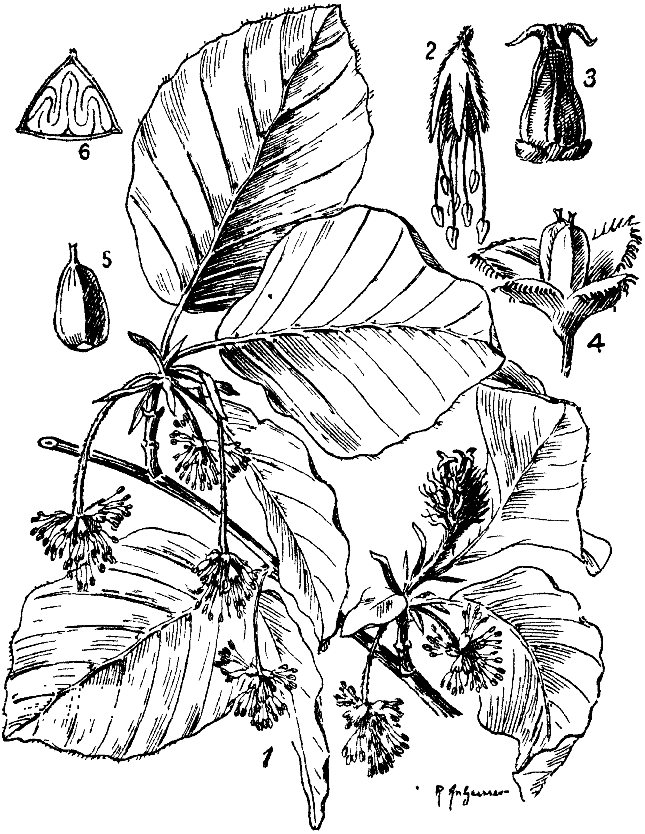


FIG 663 —*Fagus sylvatica* (⅔ nat size) 1 Branch with male and female inflorescences 2 Male flower 3, Female flower 4 Open cupule with two fruits 5 Fruit 6 Transverse section of a fruit showing the folded cotyledons of the embryo (2 3 6 enlarged)

MORE IMPORTANT SPECIES —*Fagus sylvatica*, the Beech (Fig 663), is one of our most important deciduous trees The leaf is entire, elliptical, shortly stalked, and, especially when young, covered with fine hairs Leaves two ranked. Inflorescences on shoots of the current season Male inflorescences capitate and pendulous, flowers with an oblique, bell shaped perianth and usually 8 12 stamens Female inflorescences terminal, capitate and erect, flowers in two flowered dichasia The cupule surrounds both flowers (Fig 664 *B*), and completely envelops the triangular, nut like fruits, at maturity it opens by splitting into four valves Its surface is covered with numerous, blunt prickles

Castanea vulgaris, the edible Chestnut, is a native of the Mediterranean region. The inflorescences on shoots of the current year bear in some cases only male flowers, in others female flowers at the base and male flowers above. Flowers grouped in dichasia. Female dichasia three-flowered (Fig. 664 *A*), so that three nuts come to be enclosed within the spiny cupule, which splits into four valves. The Oaks, *Quercus pedunculata* (Figs. 665, 666) and *Quercus sessiliflora*, are the largest deciduous trees of European woods. Leaves oval, margins sinuately lobed. The pendulous male inflorescences spring, at the time that the new foliage is expanding, from axillary buds of the shoot of the preceding year or from the lowest buds of the shoot of the current year; flowers solitary, consisting of a perianth of 5-7 segments and 6-12 short stamens. Female inflorescences erect, few-flowered, in the axils of the upper leaves of the shoot of the current year. Flowers in three-flowered dichasia, the lateral flowers of which are suppressed. The remaining central flowers in *Q. pedunculata* with long stalks, in *Q. sessiliflora* sessile. Each flower is invested by a cupule (Fig. 664 *C*), which is at first inconspicuous, but is fully developed on the ripe fruit.

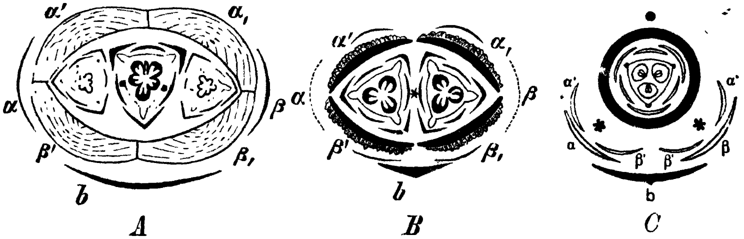


FIG. 664.—Diagrams of the female dichasia of: *A*, *Castanea vulgaris*; *B*, *Fagus sylvatica*; *C*, diagram of the single flower of *Quercus pedunculata*. *b*, Bract; *α β*, bracteoles; *α*, *β,*, *α' β'*, bracteoles of the secondary flowers adherent to the cupule. (*A*, *B*, after EICHLER. *C*, after PRANTL-FROLL.)

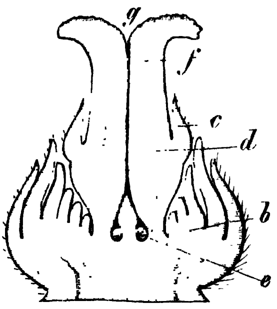


FIG. 665.—*Quercus pedunculata*, longitudinal section of the female flower. *b*, The young cupule; *e*, ovule; *d*, ovary; *c*, perigone; *f*, style; *g*, stigma. (After BERG and SCHMIDT, magnified.)

The Beech yields firewood, tar, and pyroligneous acid; the Oak provides a valuable timber, a bark containing tannin used in tanning, and cork from the Cork-oak.

OFFICIAL.—The GALLS (GALLA) produced on the young twigs of *Quercus infectoria* as a result of puncture by the Gall-wasp, *Cynips tinctoria*; Tannic Acid is obtained from these. *Betula lenta* yields OLEUM GAULTHERIAE.

Order 1. Polycarpicae

Sub-Order 2. Ranales

Returning to the consideration of Order 1. Polycarpicae (p. 623), the second Sub-order Ranales has to be described here.

In this Sub-order, which comes under the general description of the Polycarpicae on p. 623, the flowers are for the most part brightly coloured and entomophilous: the Ranales include herbaceous forms, sometimes amphibious or aquatic and exhibit close connections with the Monocotyledons (23a). The families placed first, like the Lauraceae in the Sub order Magnoliales, are provided with a trimerous perianth and three whorls of stamens.

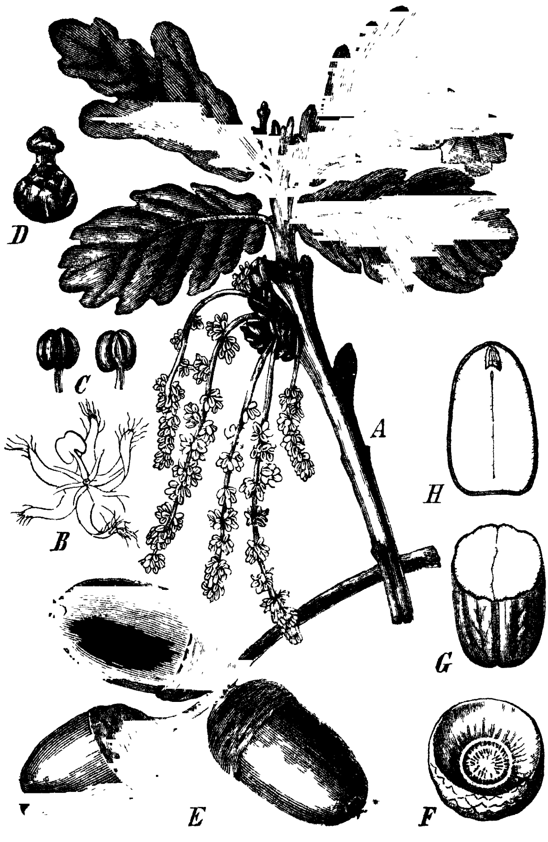


FIG 666.—*Quercus pedunculata* *A*, Flowering branch *B*, a male flower (magnified), *C*, stamens (magnified), *D*, a female flower (magnified) *E* infructescence, *F*, cupule, *G H*, seed (After SCHIMPER.)

Family 1. **Berberidaceae.** Hermaphrodite flowers, with a perianth of two trimerous whorls, two or more trimerous whorls of stamens and one carpel, bearing the ovules on the ventral suture. In *Berberis vulgaris* the leaves on the shoots of unlimited growth are transformed into spines.

OFFICIAL.—PODOPHYLLI RHIZOMA obtained from the North American Berberidaceous plant, *Podophyllum peltatum* (Fig. 667), *P. emodi*, yields PODOPHYLLI INDICAE RESINA and RHIZOMA. *Berberis aristata* yields BERBERIS.

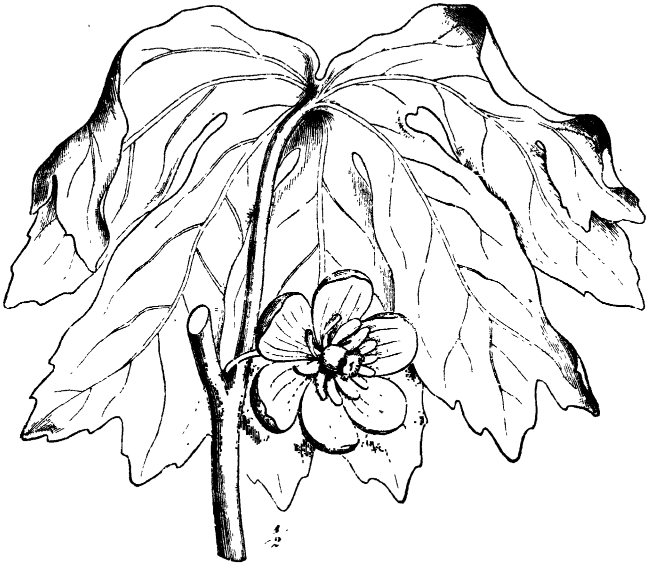


FIG. 667.—*Podophyllum peltatum* (½ nat. size). (From *Nat. Pflanzenfamilien.*)

Family 2.—**Menispermaceae.**—Abundant in the tropics; mostly climbers. Flowers trimerous, with three carpels.

OFFICIAL.—CALUMBAE RADIX from *Jateorhiza Columba*, a twining plant of tropical East Africa.

Family 3. **Nymphaeaceae.**—Aquatic plants with submerged or floating leaves, the latter often of very large size; the vegetative organs contain latex (Figs. 668-670). The origin of the Monocotyledons is to be sought in the neighbourhood of this family.

Cabomba aquatica has trimerous flowers, with a perianth of two whorls, two whorls of stamens and three carpels (Fig. 670). Its shoots have divided, submerged leaves, and entire floating leaves which appear at the time of flowering. The possession of laticiferous tubes is characteristic.

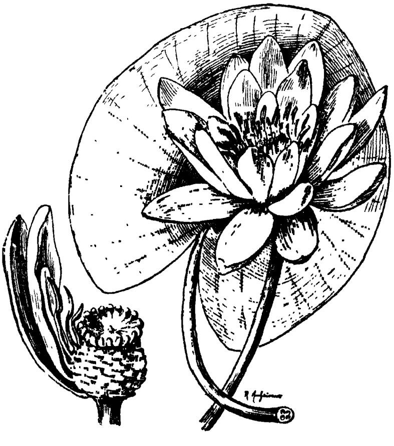


FIG. 668.—*Nymphaea alba* (½ nat. size). The spiral arrangement of the stamens and petals is shown by their insertions on the ovary to the left.

Nymphaea alba, the White Water Lily (Figs. 668, 669), has large, floating leaves and white flowers, protected by firm green sepals. Within the corolla comes the zone of numerous stamens and the inferior ovary composed of numerous coherent carpels. The spiral arrangement of the members of the perianth and androecium is seen by the scars of their insertion when they are removed from the inferior ovary (Fig. 668), and in the floral diagram (Fig. 669). In *Nuphar* the ovary is superior and the small petals bear nectaries ; the conspicuous calyx renders the

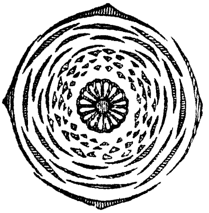


FIG. 669.—*Nymphaea*. Floral diagram (After NOLL.)

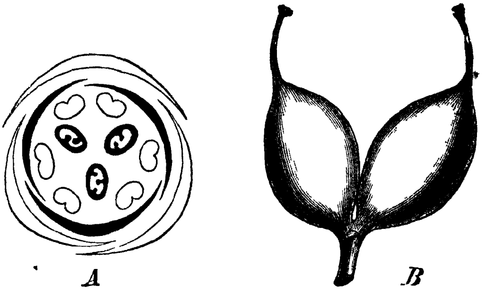


FIG. 670.—*A*, Floral diagram. *B*, Fruit of *Cabomba aquatica* showing two carpels developed as partial fruits. (× 4. After BAILLON.)

flower attractive. In *Nelumbium*, both the leaves and flowers are raised above the surface of the water. *Victoria regia* from the Amazon, and *Euryale ferox* from tropical Asia, have gigantic floating leaves ; they are often cultivated in Botanic Gardens. The flowers of the former are beetle-pollinated, while the latter is autogamous.

Family 4. **Ranunculaceae.**—The plants belonging to this family

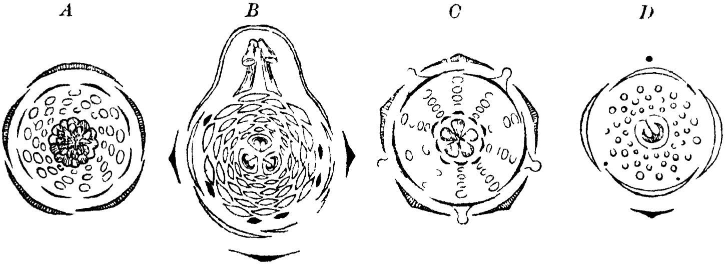


FIG. 671.—Floral diagrams of Ranunculaceae. *A*, *Adonis autumnalis*. *B*, *Aconitum napellus*. *C*, *Aquilegia vulgaris*. *D*, *Cimicifuga racemosa*. (After EICHLER.)

are annual herbs (*Myosurus*), more commonly perennial herbs (*Caltha*), or rarely low or climbing woody plants (*Clematis*, species of *Paeonia*) with alternate, exstipulate leaves. Flowers hermaphrodite, the members in many cases arranged spirally ; this is very evident in *Myosurus* and where the stamens and the carpels are numerous (Figs. 671, 672). Perianth either forming a simple or double perigone (*Aconitum*), or differentiated into calyx and corolla (*Ranunculus*). Stamens indefinite. Pollen-grains with at least three places of exit for the pollen-tubes. Carpels three to indefinite, borne on the convex receptacle (Fig. 672), and forming an apocarpous, superior ovary. Ovules, borne on the ventral suture, singly or in numbers. The partial fruits are follicles (*Paeonia*), achenes (*Anemone*), or berries (*Hydrastis*). Seed with a small embryo enclosed within the large, oily endosperm (Fig. 673).

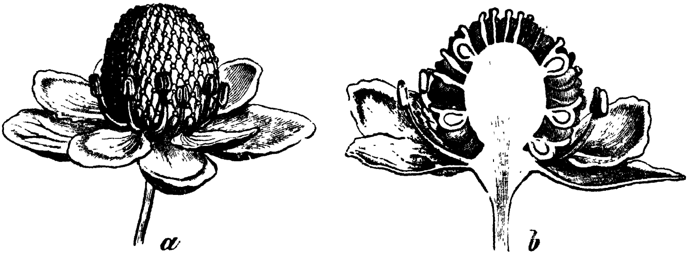


Fig. 672.—*a*, Flower of *Ranunculus sceleratus*; *b*, the same, cut through longitudinally; magnified. (After Baillon.)

Important Genera.—Many of our commonest meadow and woodland plants belong to this order. They are all in greater or less degree poisonous. A number of species of *Ranunculus*, characterised by the usually yellow flowers, convex receptacle, and fruit composed of numerous free achenes, occur in Britain. The petals have a nectary at the base. Leaves palmately divided more or less deeply. *R. sceleratus* is very poisonous (Figs. 672, 674). *R. arvensis* with large, spiny achenes or nutlets (Fig. 673). The aquatic species of *Ranunculus*, belonging to the section *Batrachium*, are often heterophyllous (Fig. 135), the floating leaves serving, as in *Cabomba*, to support the flowers above the surface of the water.

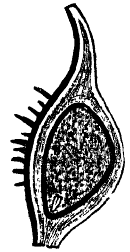


Fig. 673. — *Ranunculus arvensis*. Carpel in longitudinal section. (Enlarged. After Baillon.)

Species of *Anemone* are also widely distributed in Europe. *A. nemorosa* occurs commonly in woods and is one of our early spring flowers. It has a horizontal, subterranean rhizome, which terminates in a flower, the further growth of the plant being carried on by a lateral shoot. Perianth simple, petaloid. All species of *Anemone* have, at a greater or less distance from the perianth, a whorl of, usually, three leaves forming an involucre (Fig. 675). In *A. hepatica* this stands just below the perianth and thus resembles a calyx. All the species are to some extent poisonous, especially *A. Pulsatilla* (Fig. 675). The plants of the genus *Clematis* are mostly woody and differ from other Ranunculaceae in having opposite leaves. Many species are cultivated. *C. vitalba* is one of our few native lianes. The achenes of the species of *Clematis* and of many kinds of *Anemone* are provided with hairy or feathery appendages, which facilitate their distribution by the wind. *Caltha palustris*, the Marsh Marigold (Fig. 676), is one of the most conspicuous spring flowers in damp meadows. Perianth simple, bright yellow. Leaves cordate or reniform, short-stalked, with erect sheathing base. Fruit, as in the species of *Helleborus* that flower in the winter, composed of follicles. The

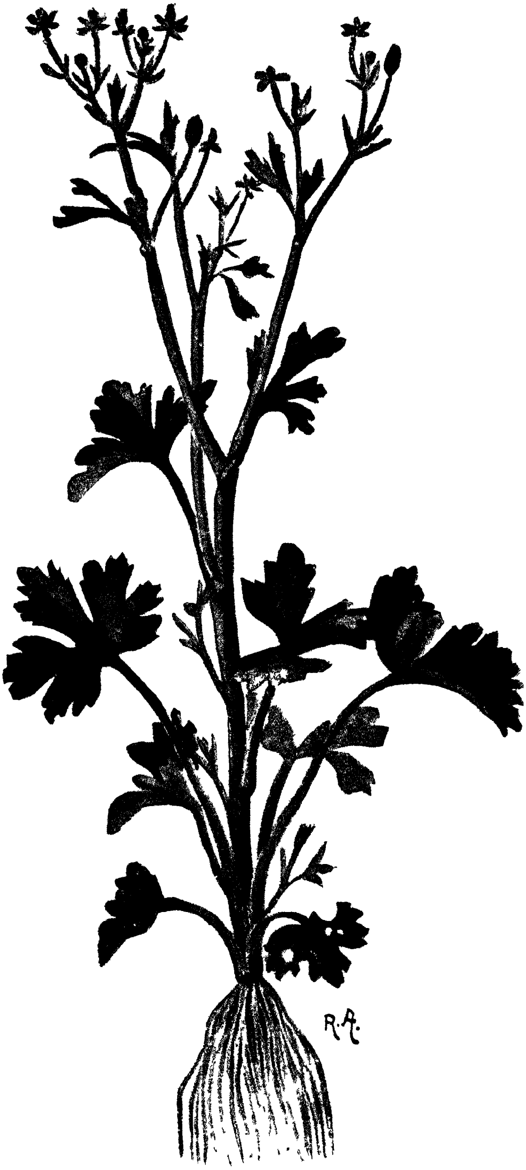


FIG. 674 —*Ranunculus sceleratus* (½ nat. size). *POISONOUS.*

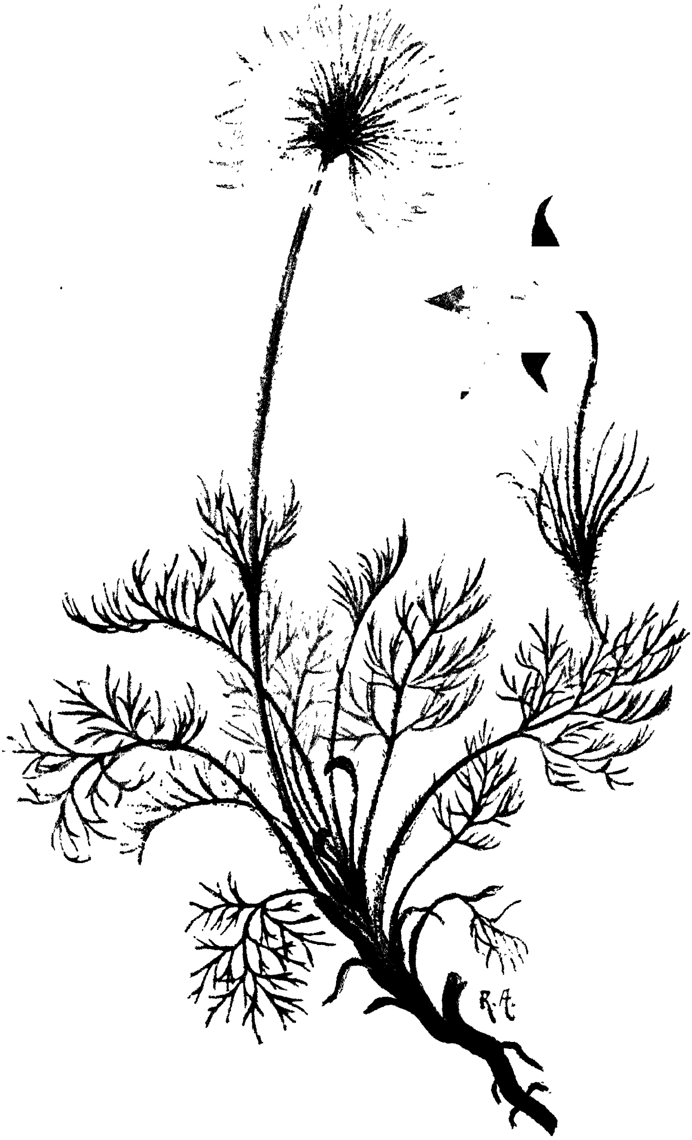


FIG. 675.—*Anemone Pulsatilla* (½ nat. size). *POISONOUS.*

Monkshood (*Aconitum napellus*) (Fig. 677 *A*, *B*) is a stately perennial herb with underground tubers and occurs most commonly in alpine meadows. The leaves are palmately divided, the segments being in turn pinnately lobed. Inflorescence a dense raceme, reinforced by lateral inflorescences standing in the axils of the upper leaves. Flowers zygomorphic. One of the five dark-blue sepals is helmet-shaped, and protects two long-stalked, tubular, two-lipped nectaries, which (as in *Helleborus* and *Eranthis*) correspond to petals. The remaining petals are wanting or are reduced to inconspicuous, narrow structures. *Aconitum Lycoctonum* has smaller yellow flowers of similar construction. All the species are poisonous. *Aquilegia*, *Delphinium*, and *Paeonia* are favourite ornamental plants with showy flowers. In *Actaea* and *Hydrastis* the fruit is a berry.

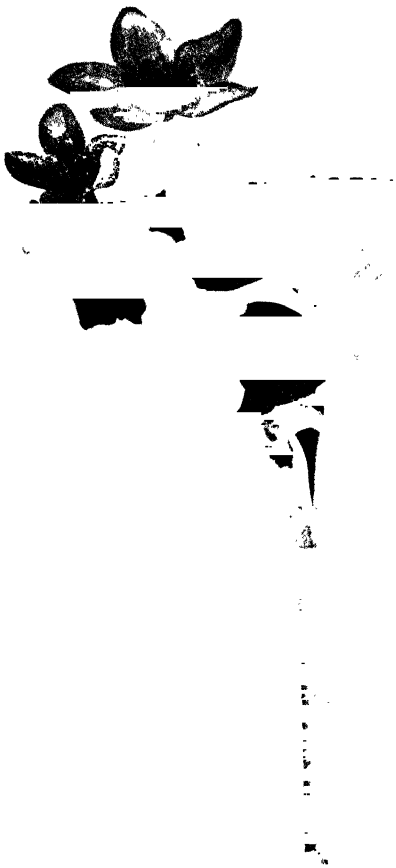


Fig. 676.—*Caltha palustris* (⅔ nat. size). *Poisonous.*

OFFICIAL. — ACONITI RADIX is obtained from *Aconitum napellus*. STAPHISAGRIAE SEMINA from *Delphinium staphisagria*. HYDRASTIS RHIZOMA from the North American *Hydrastis Canadensis*, a perennial herb which sends its subaerial shoots up from the subterranean rhizome; the base of the shoot has keeled scale-leaves in two ranks. The flowers are solitary and terminate the shoots, each of which bears two foliage-leaves. The simple white perianth falls when the flower opens. The androecium and the apocarpous gynaeceum consist of numerous members. The fruit consists of numerous small berries, each of which includes 1-2 seeds. The alkaloid HYDRASTINE is obtained from the rhizome.

Order 11. Rhoeadales

Herbs, or more rarely shrubs, with alternate, exstipulate leaves. Flowers hermaphrodite, cyclic; whorls usually bimerous. Ovary superior, unilocular. Placentas on the united margins of the carpels, projecting more or less into the cavity (Fig. 678). Stigmas com-

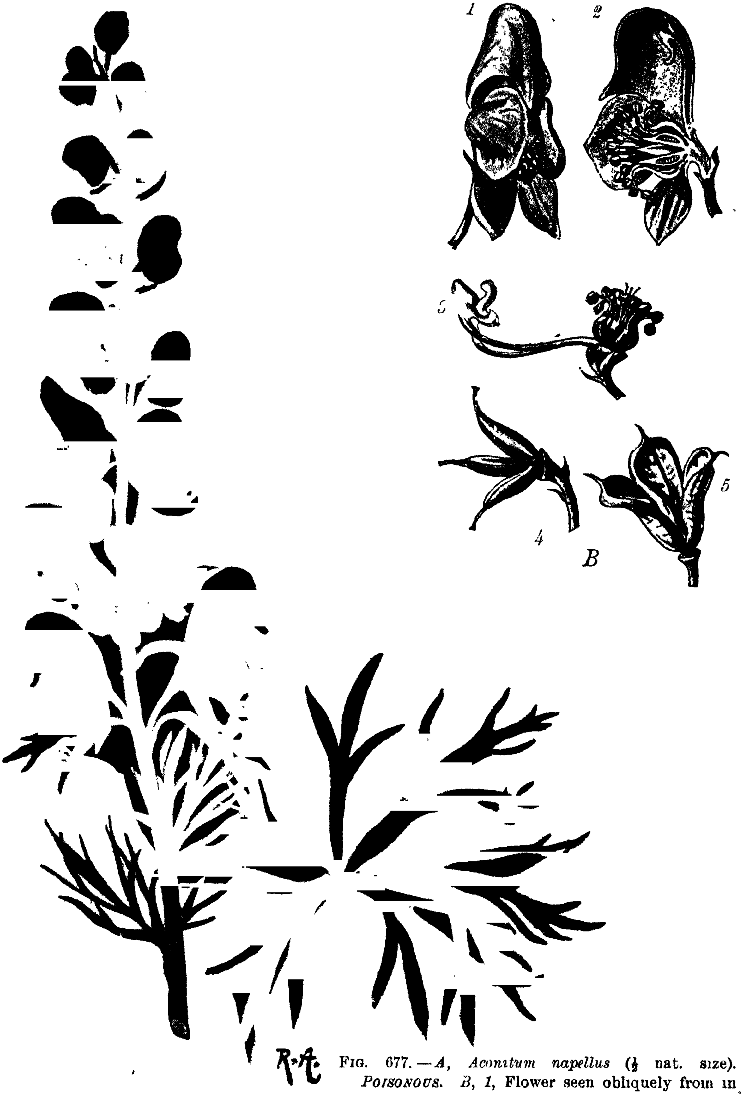


FIG. 677.—*A*, *Aconitum napellus* (½ nat. size). POISONOUS. *B*, *1*, Flower seen obliquely from in front. *2*, Flower in longitudinal section. *3*, The nectaries, formed from petals, and the androecium after the perigone has been removed. *4*, Fruit composed of three apocarpous carpels. *5*, Follicles opened.

misural, *i.e.* situated immediately over the sutures. Dehiscence of the fruit by separation of the middle portions of the carpels from the persistent placentas.

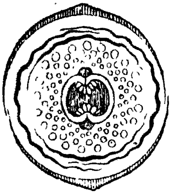


Fig. 678.—Floral diagram of *Glaucium* (Papaveraceae). (After Eichler.)

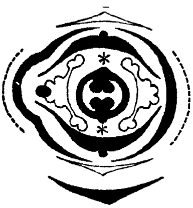


Fig. 680.—Floral diagram of *Corydalis cava.* (After Eichler.) At the base of the stamen standing above the spur is a nectary.

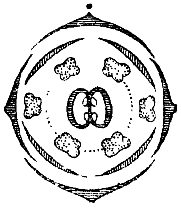


Fig. 681.—Cruciferae. Floral diagram (*Brassica*). (After Noll.)

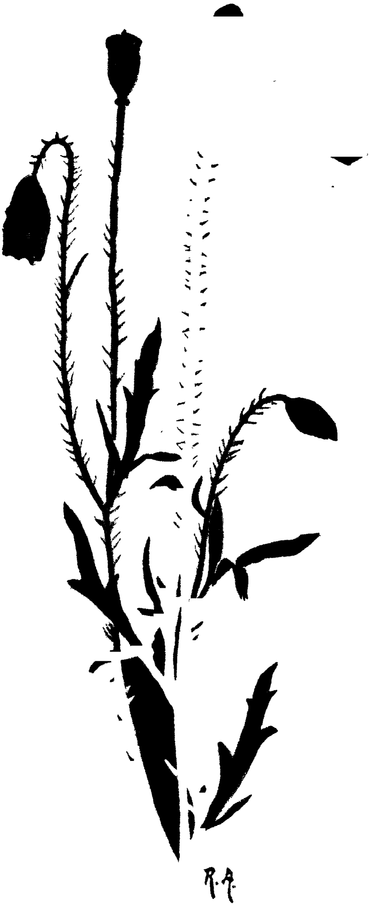


Fig. 679.—*Papaver Rhoeas.* (½ nat. size.)

The relationship of the families grouped in this Order is confirmed serologically. The occurrence of systems of tubes with various contents is noteworthy.

Family 1. **Papaveraceae** (34).—This family connects the order to the Polycarpicae by such characters as the presence of laticiferous tubes (Nymphaeaceae), occurrence of trimerous flowers in *Bocconia* (Berberidaceae), the stigmas situated directly above the carpels and the occasional occurrence of an apocarpous gynaeceum (*e.g. Platystemon*). The increase in number of stamens is brought about by chorisis; they are cyclic. The seeds have abundant endosperm.

Chelidonium majus, Celandine, has yellow latex and a bicarpellary ovary. *Ch. laciniatum* is a mutant of *Ch. majus*. A number of species of *Escholtzia*, *Argemone*, and *Papaver* are cultivated as ornamental plants. *Papaver Rhoeas*, the Poppy (Fig. 679), is a common weed in corn-fields. The bent position of the flower-bud is characteristic. *Papaver somniferum*, which is of Oriental origin, has abundant white latex The ovary is unilocular, and in the ripe fruit the separation of the central portion of each carpel from the placentas at dehiscence is limited to the tips of the carpels. These portions bend outwards just below the flat stigmatic expansion; and the kidney-shaped seeds are thrown out of the small openings when the capsule, borne on its long stalk, is moved by the wind.

OFFICIAL.—*Papaver somniferum*, the Opium Poppy, yields OPIUM and CODEINA. *Papaver Rhoeas* yields RHOEADOS PETALA.

Family 2. **Fumariaceae.**—This small family is of interest on account of the occurrence of transversely zygomorphic flowers in *Corydalis* (Fig. 680) and a bi-symmetrical corolla with two spurs in *Dicentra spectabilis*. The fruits are nutlets in *Fumaria* and capsules in *Corydalis* and *Dicentra*. Seeds with endosperm.

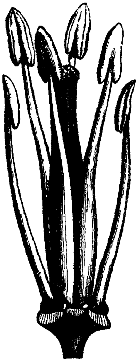


FIG. 682.—*Cardamine pratensis*. Flower with perianth removed. (× 4. After BAILLON.)

Family 3. **Cruciferae** ([35]).—This family is mainly distributed in the northern hemisphere. Annual, biennial, or perennial herbs without milky juice. Inflorescence racemose, usually without bracts or bracteoles. Flowers actinomorphic, always lateral, composed of bimerous whorls. Floral formula, K 2 + 2, C 4, A 2 + 4, G $\underline{(2)}$ (Fig. 681). The outer whorl of sepals stands in the median plane; the four petals alternate with the sepals. The two outer stamens are shorter than the four inner ones which stand in the median plane (p. 119). The latter correspond to two stamens branched to the base. The carpels form a superior, usually pod-like, ovary, which is divided into two chambers by a false septum (p. 556), stretching between the parietal placentas (Fig. 683 *A*, *C*, *D*). The fruit opens by the separation from below upwards of the main portion of each carpel, leaving the seeds attached by their stalks to the central portion formed by the placentas together with the false septum. Rarely the fruit is indehiscent (*e g. Isatis*). Embryo curved. Endosperm wanting or reduced to a single layer of cells coherent with the seed-coat (Figs. 684, 685).

The number of species and their abundance make the Cruciferae one of our most important native families of flowering plants. Their brightly coloured, mostly yellow, flowers render them conspicuous in various situations and at all periods of the year. The nectaries, which are borne on the receptacle at the base of the stamens, also show that the flowers are entomophilous. The family includes a number of economic plants and others cultivated for their flowers.

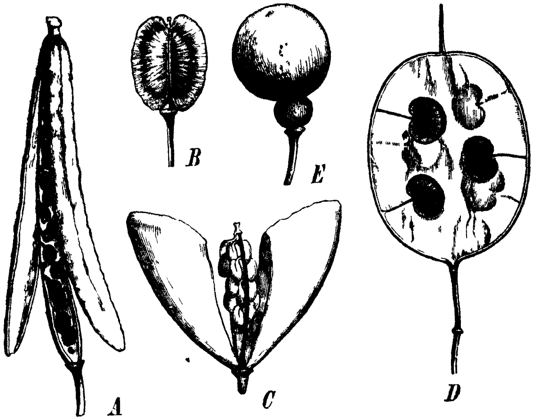


FIG. 683.—Cruciferous fruits. *A*, *Cheiranthus cheiri*; *B*, *Lepidium sativum*; *C*, *Capsella bursa pastoris*; *D*, *Lunaria biennis*, showing the septum after the carpels have fallen away. *E*, *Crambe maritima*. (After BAILLON.)

Cheiranthus Cheiri, the Wallflower (Fig. 683 *A*). *Matthiola*, the Stock.

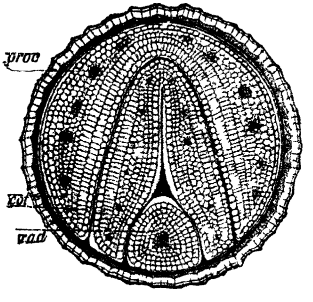


FIG. 684.—Transverse section of the seed of *Brassica nigra*. *rad*, radicle; *cot*, cotyledons; *proc*, vascular bundles (After MOLLER.)

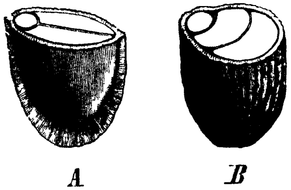


FIG. 685.—Seeds of Cruciferae cut across to show the radicle and cotyledons. *A*, *Cheiranthus cheiri* (× 8); *B*, *Sisymbrium alliaria* (× 7). (After BAILLON.)

Numerous species of *Brassica* have been long in cultivation; *B. oleracea*, the Wild Cabbage, in its various forms (*a*) *sylvestris*, which occurs on the coasts of Northern Europe and is to be regarded as the wild form; (*b*) *acephala*, Borecole or Kale; (*c*) *gonglyodes*, Turnip-rooted Cabbage; (*d*) *gemmifera*, Brussels Sprouts; (*e*) *sabauda*, Savoys; (*f*) *capitata*, the Cabbage; (*g*) *botrytis*, Cauliflower and Broccoli. *Brassica campestris*, with the cultivated forms—(*a*) *annua*, (*b*) *oleifera*, (*c*) *rapifera*. *Brassica napus*, the Turnip—(*a*) *annua*, (*b*) *oleifera*, (*c*) *napobrassica*. *Brassica nigra*, Black Mustard (Fig. 686), an annual plant, was cultivated even in ancient times. The radical leaves are long-stalked and lyrate with rounded terminal lobes; on ascending the copiously-branched stem they become lanceolate and gradually smaller. The plant is glabrous except for some bristly hairs on the upper surface of the leaf. Inflorescence a raceme; the bright yellow flowers stand out from the main axis, while the developing fruits are erect and applied to the axis. *Sinapis alba*, White Mustard, is a hairy plant, distinguishable from the Black Mustard by the long broadly-beaked fruits, the valves of which bear coarse bristly hairs. The fruits project from the axis of the inflorescence. The seeds are yellowish-white and twice as large as those of *Brassica nigra*. *Anastatica hierochuntica*, Rose of Jericho, is an annual desert plant of North Africa characterised by the hygroscopic movements of its branches (cf. p. 335). *Crambe* (Fig. 685 *E*), with the lower portion of the silique sterile, and *Cakile* are thick-leaved strand plants. *Raphanus sativus*, the Radish. *Vesicaria*, *Aubrietia*, *Draba*, *Lunaria* (Fig. 683 *D*). *Cochlearia officinalis*, Scurvy Grass. *Erophila*, *Iberis* with somewhat zygomorphic flowers. *Capsella bursa pastoris*, Shepherd's purse (Fig. 683 *C*). *Isatis tinctoria*, Woad.

OFFICIAL.—OLEUM SINAPIS VOLATILE, from *Brassica nigra*. ARMORACIAE RADIX, from *Cochlearia Armoracia*.

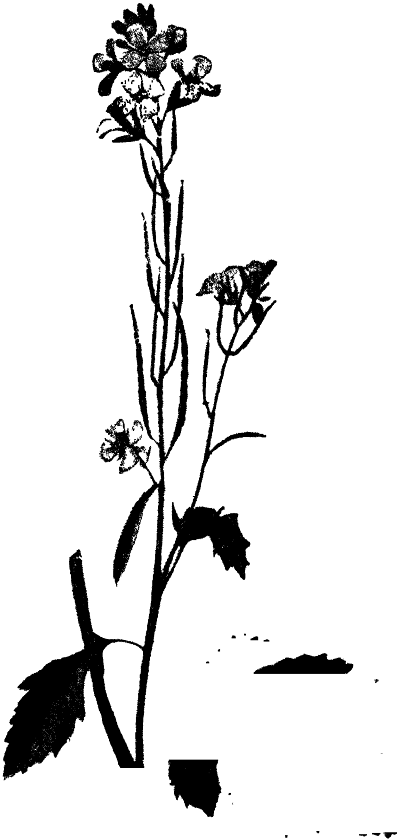


FIG. 686.—*Brassica nigra*. (½ nat. size.)

Family 4. **Capparidaceae.**—*Capparis spinosa* is a small shrub occurring on rocky ground in the Mediterranean region. The leaves are simple with short, recurved, spiny stipules. The actinomorphic flowers are axillary and solitary; the androecium by chorisis consists of numerous members. In this respect and in the presence of a gynophore which raises the pistil above the rest of the flower (Fig. 687), there are differences from the Cruciferae. The fruit is a berry which reaches the size of a plum and contains numerous seeds. Capers are prepared from the young flower-buds.

Order 12. Parietales

The plants belonging to this order are characterised by their usually regular, pentamerous flowers; the stamens are increased in number by chorisis, or, when the separation of the branches is incomplete, they form distinct bundles; the superior ovary is usually trimerous. The relationship to the Rhoeadales is rendered probable by serodiagnostic investigations.

a, Placentation parietal.

Family 1. **Cistaceae.**—Pentamerous, regular flowers, with numerous stamens and three to five carpels united to form a unilocular or multilocular ovary with parietal placentas. In Britain the Rock Rose (*Helianthemum vulgare*) (Fig. 688).

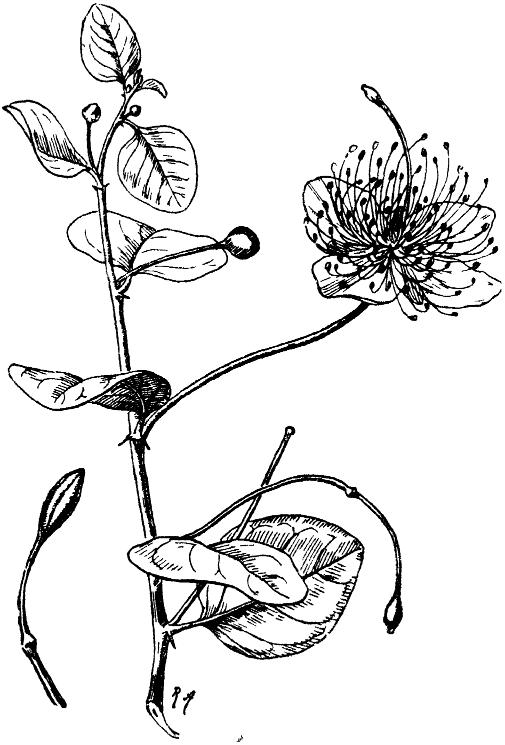


Fig. 687.—*Capparis spinosa.* Flowering branch and a young fruit borne on the gynophore. (⅔ nat size)

Many species of *Cistus* are characteristic shrubs of the vegetation of the Mediterranean region.

Family 2. **Droseraceae.**—Includes the Sundew (*Drosera*) and similar plants; these capture insects by means of their tentacles with viscid heads, and digest them.

Family 3. **Violaceae.**—Distinguished by dorsiventral flowers with only five stamens. Ovary unilocular. The flowers have the anterior petal prolonged backwards as a spur, into which two nectar-secreting processes of the two anterior stamens project (Fig 689).

b, Placentation axile (usually separated as Guttiferales).

Family 4. **Ternstroemiaceae** have a gradual transition from sepals to petals, like that found in the Magnoliaceae, numerous stamens, and a trilocular ovary with axile placentation. The Tea-plant (Fig. 690) and the Camellia belong to this family.

Family 5. **Guttiferae.**—Distinguished by the schizogenous glands and the union in bundles of the stamens. *Hypericum* is a British representative. The red contents of the secretory organs of *Garcinia Hanburyi* when dried form Gamboge.

Family 6. **Dipterocarpaceae.**—Characterised by the great enlargement of some or all the sepals after fertilisation. *Dryobalanops Camphora* yields Borneo Camphor. Dammar is obtained from *Shorea Wiesneri.*

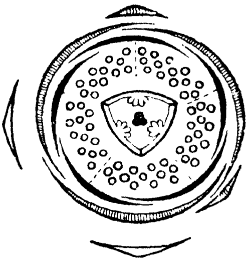


FIG. 688.—Floral diagram of *Helianthemum vulgare* (Cistaceae). (EICHLER.)

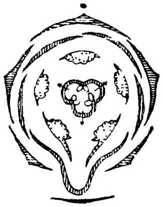


FIG. 689.—Floral diagram of *Viola.* (After NOLL.)

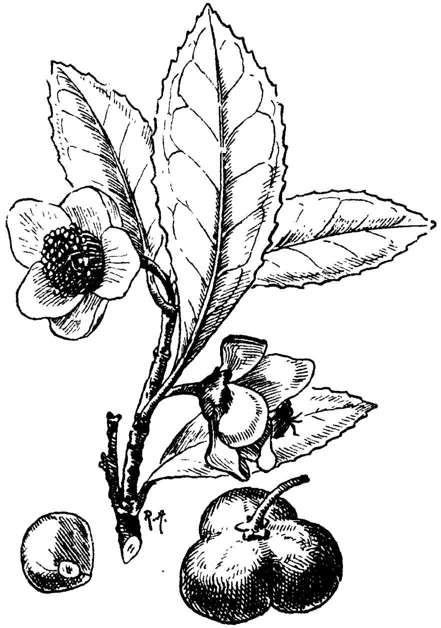


FIG. 690.—*Thea chinensis.* Flowering shoot ($\frac{2}{3}$ nat. size); fruit and seed.

Order 13. Rosales

The cyclic flowers are in other respects similar to those of the Polycarpicae; the connection of the Rosaceae with the Calycanthaceae and Ranunculaceae is particularly close. The single carpel in the Pruneae and the dorsiventral flowers of the Chrysobalaneae lead on to the Leguminosae.

The order includes plants of very diverse form and construction with alternate leaves. The flowers are almost always actinomorphic with the members arranged in whorls; they have five, ten, or numerous stamens and carpels, the pistil is as a rule apocarpous. The large part played by the floral axis in the construction of the flower and fruit is characteristic. K5, C5, A5–∞, G1–∞.

The connection of the Rosales on the one hand with the Polycarpicae and on the other with the Leguminosae and Myrtales has been confirmed serologically.

Family 1. **Crassulaceae.**—Succulent herbs or under-shrubs with cymose inflorescences. *Sedum* (Fig. 691) with pentamerous flowers; there are a number of British species. *Sempervivum* (35a), flowers with from six to an indefinite number of members in the whorls. *Bryophyllum* with tetramerous flowers, noteworthy on account of the abundant formation of buds in the indentations of the margin of the leaf. *Crassula*; South African species mimic stones by their globular form (26) (cf. Aizoaceae, p. 628).

Family 2. **Saxifragaceae.**—Herbs or woody plants with hermaphrodite, obdiplostemonous flowers. Fruit, a capsule or a berry formed of two carpels and containing an indefinite number of albuminous seeds. *Saxifraga*, Saxifrage, small herbaceous plants which are especially numerous on crags and rocky ground in mountainous districts. They have a rosette of radical leaves and bear numerous pentamerous flowers grouped in various types of inflorescence. The two partially inferior carpels are distinct from one another above. *Parnassia palustris* is common on wet moors; the pentamerous flower has four carpels. One whorl of stamens modified into palmately-divided staminodes, which serve as nectaries. The species of *Ribes* have an inferior ovary which develops into a berry, and on this account are commonly cultivated. *R. rubrum* (Fig. 692), Red Currant, *R. nigrum*, Black Currant, *R. grossularia*, Gooseberry. Other Saxifragaceae are favourite ornamental plants, *e.g.* *Ribes aureum* and *R. sanguineum*, *Hydrangea*, *Philadelphus*, and *Deutzia*.

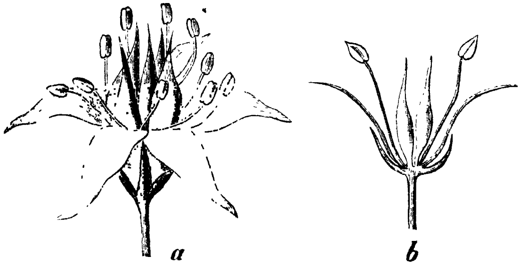


FIG. 691.—*Sedum telephium.* *a*, Flower; *b*, flower in longitudinal section. (× 4. After H. SCHENCK.)

Family 3. **Rosaceae** (36).—Characteristic features of this family are the constant presence of stipules, the absence of endosperm from most of the seeds, the apocarpous fruits, and, as a rule, the numerous stamens (Fig. 693). The two latter features are also found in the Polycarpicae and support a close relationship, but the floral members are there spirally arranged while in the Rosaceae they are in whorls, and the flowers are perigynous.

In many cases the increase in number of members of the androecium and gynaeceum proceeds from an intercalary zone of the hollowed floral axis, and continues for a considerable period. The introduction of new members is determined by the spatial relations, so that differences in the numbers of members are found in individuals of the same species.

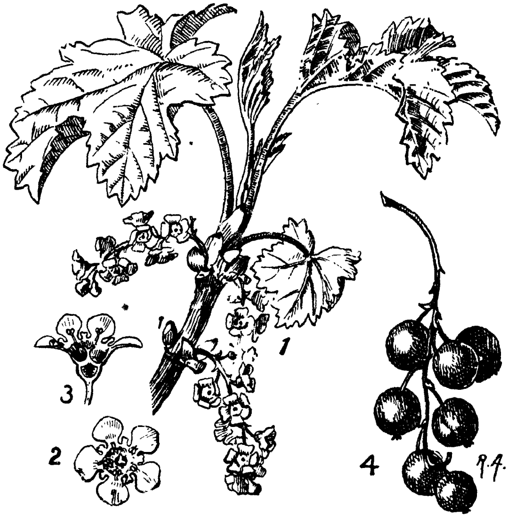


FIG. 692.—*Ribes rubrum*. (⅔ nat. size.)

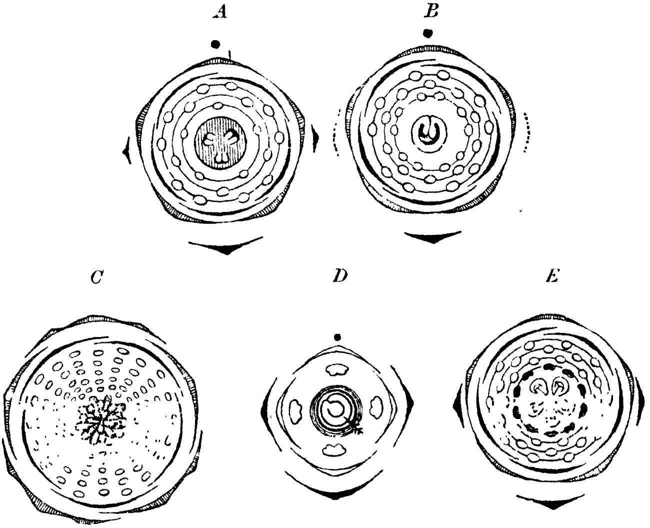


FIG. 693.—Floral diagrams of Rosaceae. *A*, *Sorbus domestica*. *B*, *Prunus Padus*. *C*, *Rosa tomentosa*. *D*, *Sanguisorba officinalis*. *E*, *Spiraea hypericifolia*. (After EICHLER.)

The genus *Spiraea* has typically pentamerous flowers with superior ovaries; many species are cultivated as ornamental shrubs (Fig. 693 *E*). *Quillaja Saponaria*

(Fig. 694), from Chili, is an evergreen tree with shortly-stalked, alternate, leathery leaves and terminal dichasia. The flower has a five-toothed, nectar-secreting disc, projecting above the large sepals. Five of the stamens stand at the projecting angles of the disc opposite the sepals; the other five are inserted opposite the petals at the inner margin of the disc. Petals narrow, white. Ovary superior. Only the middle flower of the dichasium is hermaphrodite and fertile, the lateral flowers are male and have a reduced gynaeceum. Fruit star-shaped, composed of partial fruits. Each carpel dehisces by splitting into two valves. Seeds winged.

The genera *Pyrus*, *Cydonia*, etc., are distinguished from the other Rosaceae by their inferior ovary, which usually consists of five carpels bound together by the hollow floral receptacle so that only the styles are free. The fruit resembles a berry, the floral receptacle becoming succulent. The boundaries of the separate loculi are formed of parchment-like or stony tissue. *Pyrus malus*, Apple (Fig. 546, 3), and *P. communis*, the Pear, are important and long cultivated fruit trees, of which numerous varieties are grown. *Cydonia vulgaris* the Quince, has large, solitary, rose coloured flowers. The fruits are in shape like an apple or pear, covered with fine woolly hairs and with a pleasant scent, though not edible when uncooked. In *Mespilus germanica*, the Medlar, the fruit has an apical depression surrounded by the remains of the calyx. The evergreen *Eriobotrya japonica*, is commonly planted in the Mediterranean region; *Sorbus* (*Pyrus*) *aucuparia*, the Rowan. *Crataegus oxycantha*, the Hawthorn, in hedges or planted as an ornamental tree (cf. p. 301).

FIG. 694.—*Quillaja Saponaria*. (½ nat. size. After A. MEYER and SCHUMANN.)

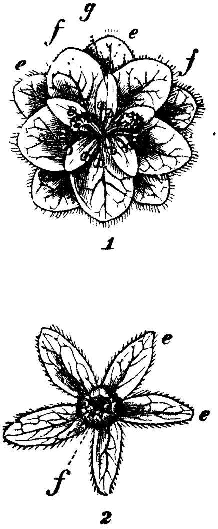


FIG. 695.—*Hagenia abyssinica*. *1*, Female flower; *e*, epicalyx; *f*, calyx; *g*, corolla (× 4). *2*, Fruit (nat size), with enlarged epicalyx. (After BERG and SCHMIDT.)

A concave, pitcher-shaped floral axis with one to many free carpels, each of which encloses 1-2 ovules, characterises the genus *Rosa*. The partial fruits are nut-like, and are enclosed by the hollowed floral axis (Fig. 693 *C*). The leafy development of the numerous stamens has given rise to the cultivated double forms. *Agrimonia* and *Hagenia abyssinica* have a dry cup-shaped receptacle. *Hagenia* is a dioecious tree from Abyssinia with unequally pinnate leaves, the adherent stipules of which render the petiole winged and channelled. Inflorescence a copiously branched panicle. Each flower has two bracteoles and an epicalyx. The flowers are unisexual by suppression of the male and female organs respectively. The corolla later falls off and the sepals become inrolled, while the epicalyx enlarges. The two free carpels have each a single ovule. Fruit one-seeded (Figs. 695, 696). *Alchemilla* has no petals (Fig. 546, 2). *Sanguisorba officinalis* has polygamous flowers, without epicalyx or corolla, aggregated in heads. Flowers tetramerous with 1-2 carpels (Fig. 693 *D*). These are greatly reduced forms.

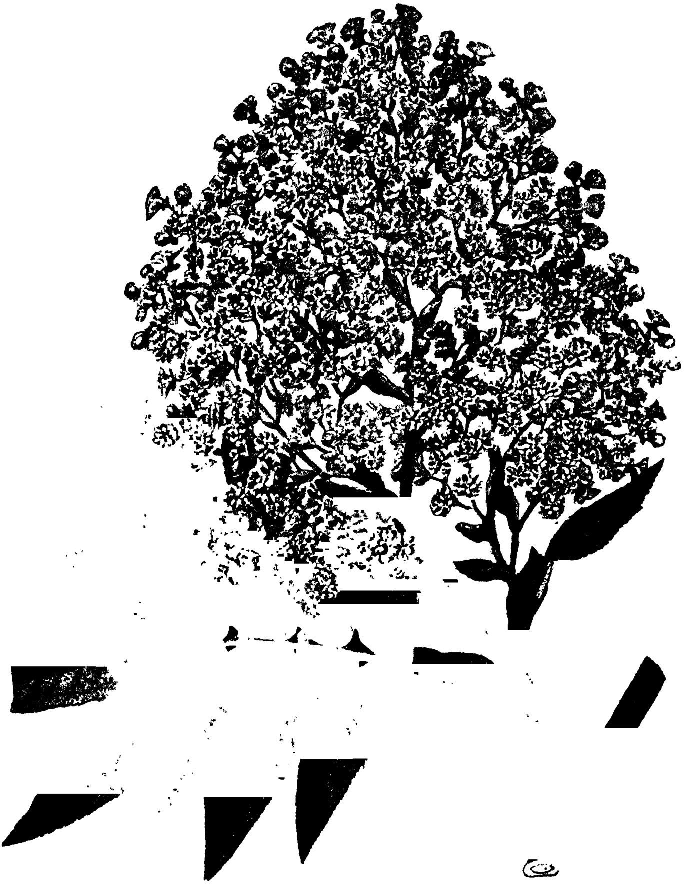


FIG. 694.—*Hagenia abyssinica* (*Brayera anthelmintica*). Inflorescence (½ nat. size). (After BERG and SCHMIDT.)

Potentilla with a number of British species has a flattened receptacle, epicalyx, and an apocarpous pistil. *Geum* and *Dryas* have hairy carpels which elongate in fruit and are distributed by the wind. *Fragraria*, Strawberry, with small achenes situated on the succulent, enlarged, floral receptacle. *Rubus*, Blackberry, has numerous species, mostly scrambling shrubs with recurved prickles. Leaves trifoliate. *R. idaeus*, the Raspberry, is one of the few species which are not straggling climbers. The small drupes are closely crowded on the convex receptacle, forming the collective fruit.

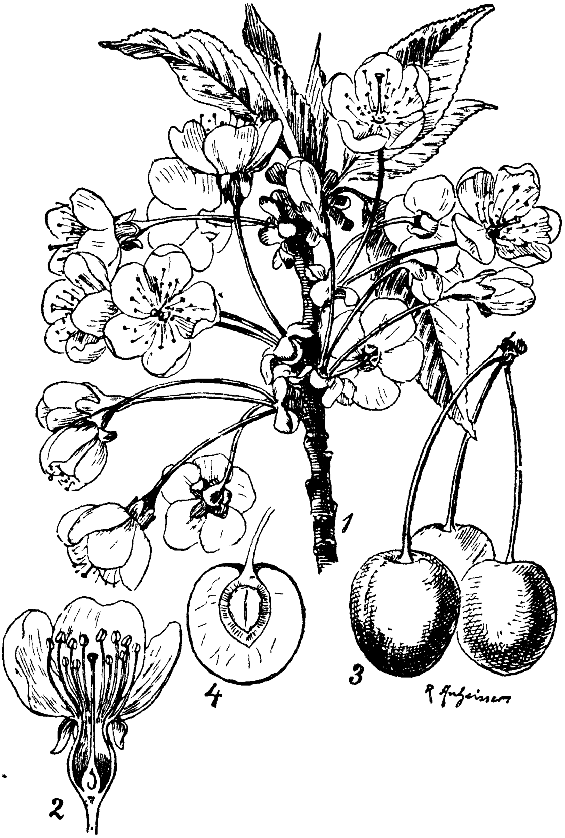


FIG. 697.—*Prunus cerasus* ($\frac{2}{3}$ nat. size). *1*, Flowering shoot; *2*, flower cut in two (slightly enlarged), *3*, fruits, *4*, fruit cut through longitudinally.

The group of the Pruneae, which includes a number of important trees bearing stone-fruits, has a single carpel situated in the middle of the flat expanded floral receptacle (Fig. 693 *B*). *Prunus cerasus*, the Wild Cherry (Fig. 697); *P. avium*, Gean; *P. domestica*, the Plum; *P. armeniaca*, the Apricot, and *P. persica*, the Peach, are of Chinese origin; *P. Amygdalus*, the Almond, from the eastern Mediterranean region. The succulent mesocarp of the Almond dries up as the fruit ripens and ruptures, setting the stony endocarp free.

POISONOUS.—The seeds of many Rosaceae contain amygdalin, but usually not in such amount as to be poisonous, owing to the resulting hydrocyanic acid, when eaten fresh in small quantity ; this is, however, often the case with the residuum left after the seeds, *e.g.* of bitter almonds, have been crushed The leaves of the Cherry Laurel (*Prunus Laurocerasus*) may also give rise to toxic effects.

OFFICIAL.—ROSAE GALLICAE PETALA from cultivated plants of *Rosa gallica* ; OLEUM ROSAE and AQUA ROSAE from *Rosa damascena*. AMYGDALA DULCIS and AMYGDALA AMARA from *Prunus amygdalus*. PRUNI VIRGINIANAE CORTEX from *Prunus serotina* LAUROCERASI FOLIA from *Prunus Laurocerasus*. CUSSO from *Brayera anthelmintica*. QUILLAIAE CORTEX from *Quillaja Saponaria*.

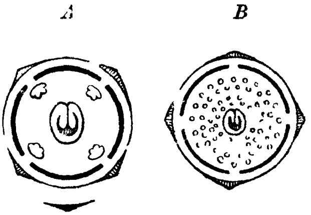


FIG. 698.—Floral diagrams of Mimosaceae. *A*, *Mimosa pudica* *B*, *Acacia lophantha* (After EICHLER.)

Order 14. Leguminosae

The common characteristic of all Leguminosae is afforded by the pistil. This is always formed of a single carpel, the ventral suture of which is directed to the dorsal side of the flower (Figs. 698, 701, 706). It is unilocular, and bears the ovules in one or two rows on the ventral suture. The fruit is usually a pod (legume), which dehisces by splitting along both the ventral and dorsal sutures. Nearly all Leguminosae have alternate, compound, stipulate leaves. Many are provided with pulvini (Fig. 698) which effect variation movements of the leaves and leaflets.

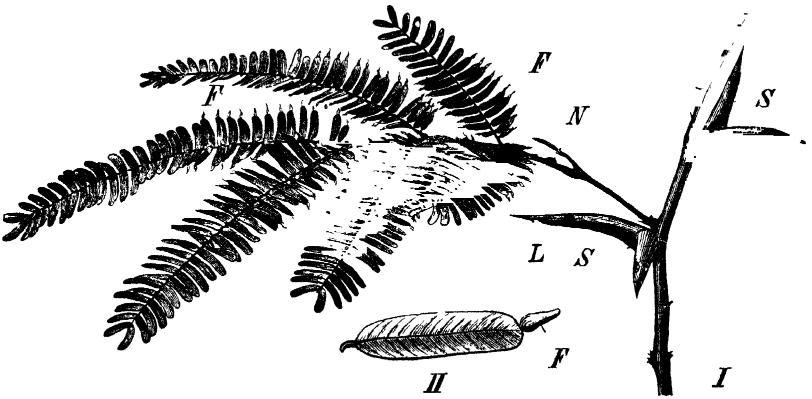


FIG. 699.—*Acacia nicoyensis*. From Costa Rica. *I*, Leaf and part of stem, *S*, hollow thorns in which the ants live, *L*, entrance, *F*, food-bodies at the apices of the lower pinnules; *N*, nectary on the petiole. (Reduced.) *II*, Single pinnule with food-body, *F*. (After F. NOLL. Somewhat enlarged.)

Family 1. **Mimosaceae.**—Trees, and erect, or climbing, shrubby plants with bipinnate leaves. Flowers actinomorphic, pentamerous, or tetramerous (Fig. 698).

Aestivation of sepals and petals valvate. Stamens free, numerous, or equal in number to the petals, or half their number. The colour of the flower is due to the

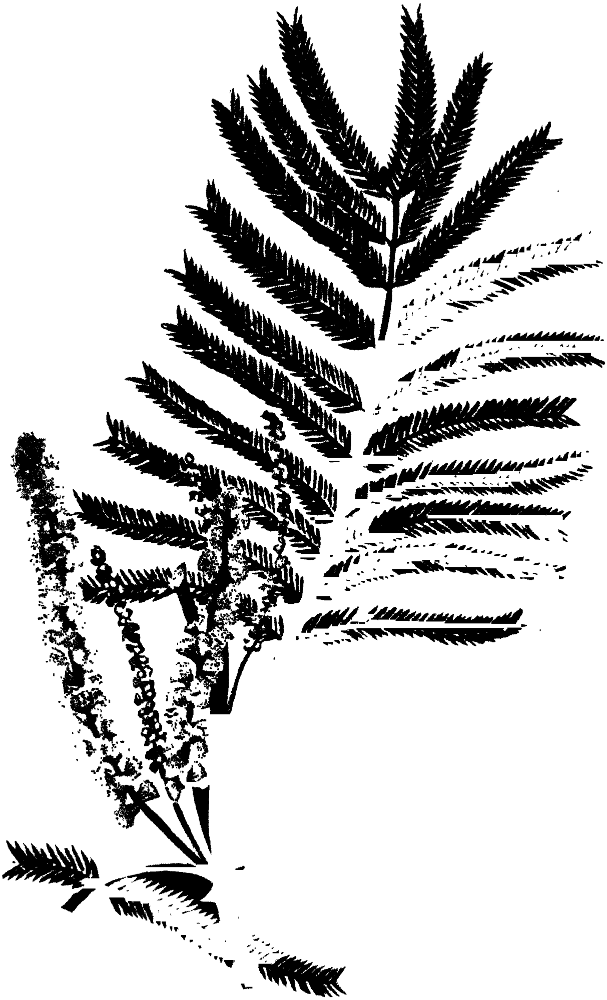


FIG. 700.—*Acacia catechu*. (⅔ nat. size. After MEYER and SCHUMANN.)

length and number of the stamens, the corolla being as a rule inconspicuous. The pollen-grains are often united in tetrads or in larger numbers. The flowers are grouped in spikes or heads. Embryo straight in the seed.

There are no representatives native to Europe of this family, which is abundant in the tropics. The Sensitive Plant (*Mimosa pudica*) (Figs. 292, 293)

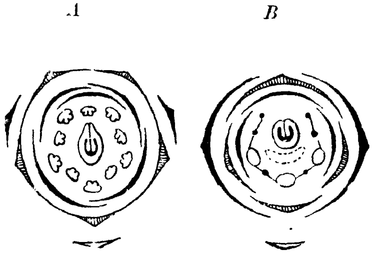


FIG. 701.—Floral diagrams of Caesalpiniaceae. *A*, *Cercis siliquastrum*. *B*, *Tamarindus indica*. (After EICHLER.)

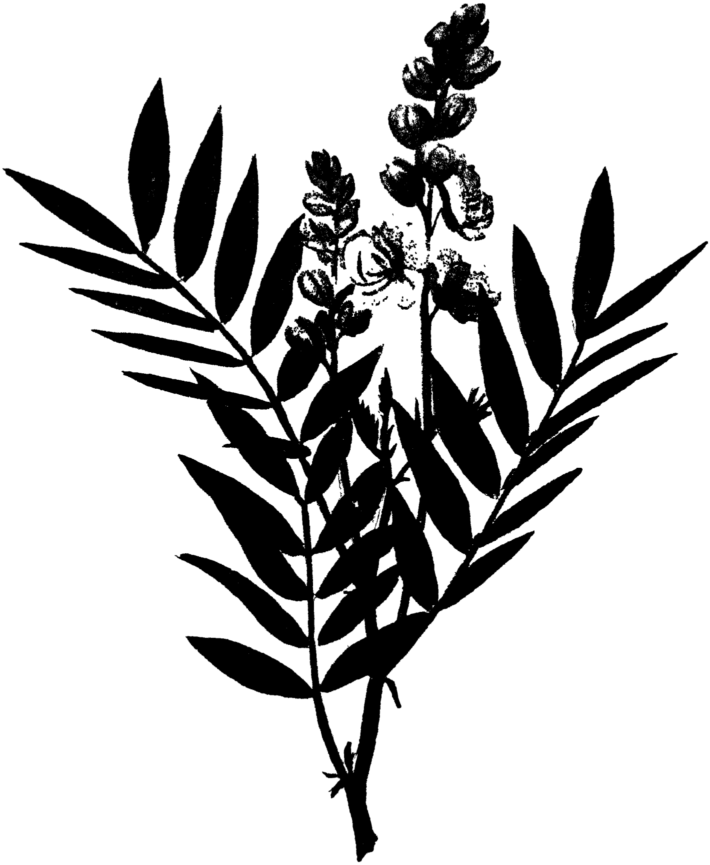


FIG. 702. *Cassia angustifolia*. (⅔ nat. size. After A. MEYER and SCHUMANN.)

occurs as a weed throughout the tropics and exhibits great irritability to contact. Numerous species of the genus *Acacia* are distributed through the tropics and sub-tropics of the Old and New Worlds. The Australian forms of the genus are frequently characterised by possessing phyllodes (p. 161), the vertical position of which contributes to the peculiar habit of the Australian forests (cf. (Fig. 185). Some American species of *Acacia* are inhabited by ants (Fig. 699)

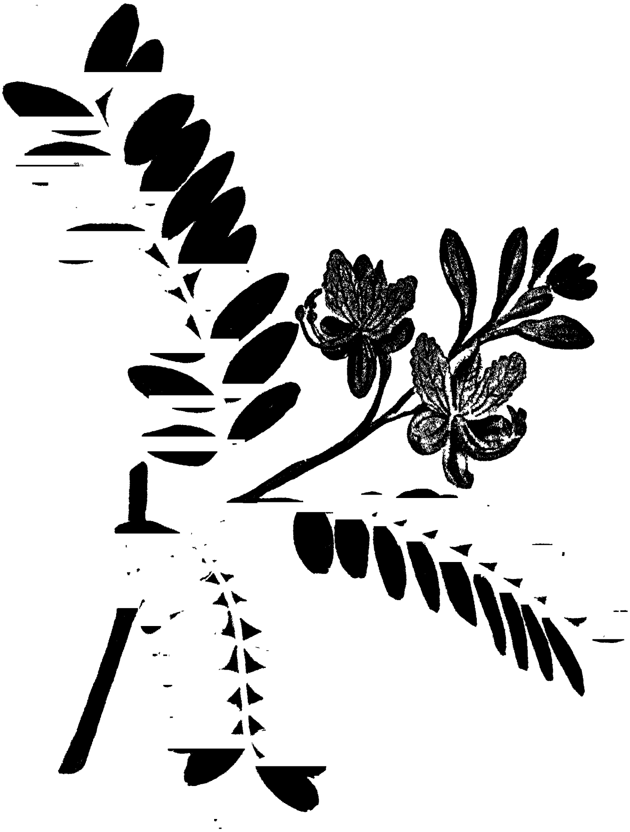


FIG. 703.—*Tamarindus indica*. (⅔ nat. size. After A. MEYER and SCHUMANN.)

which live in the large stipular thorns and obtain food from Belt's food-bodies (^{37}) at the tips of the pinnules. A mutual symbiosis has not been demonstrated in this case. Many species of *Acacia* are of considerable economic value owing to the presence of gums and tannins in the cortex, in the heart-wood, or in the pods. *A. catechu* (Fig. 700) and *A. suma* are East Indian trees from which Catechu is obtained.

OFFICIAL.—By the disorganisation of the parenchyma of the stem of *Acacia Senegal* (Soudan and Senegambia) and of other species, ACACIAE GUMMI is obtained. This exudes from wounds as a thick fluid and hardens in the air. *A. Arabica*

(Fig. 700). and *A. decurrens* yield ACACIAE CORTEX. *Acacia Catechu* yields CATECHU NIGRUM.

Family 2. **Caesalpiniaceae.**—Trees or shrubs with pinnate or bipinnate leaves. Flowers usually somewhat dorsiventral. Corolla with ascending imbricate aestivation (Fig. 701). Typical floral formula: K 5, C 5, A 5+5, G $\underline{1}$. The number of petals and stamens is often incomplete. Embryo straight Abundantly represented in the tropics and sub-tropics.

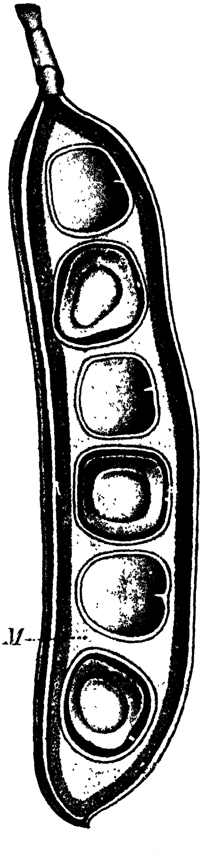


FIG. 704. — *Tamarindus indica.* Fruit in longitudinal section. *M*, the fleshy mesocarp. (After BERG and SCHMIDT.)

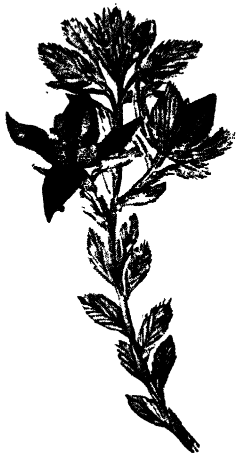


FIG. 705.—*Krameria triandra.* (⅘ nat. size. After A. MEYER and SCHUMANN.)

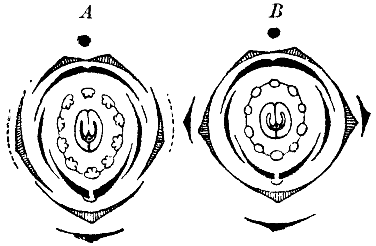


FIG. 706.—Floral diagrams of Papilionaceae. *A*, *Vicia Faba*. *B*, *Laburnum vulgare*. (After EICHLER.)

In *Cassia angustifolia* the sepals and petals are both five in number and free (Fig. 702). The lower overlapping petals are somewhat larger than the upper ones. Of the ten stamens the three upper ones are short and sterile, while the other seven, the filaments of which are curved and convex below, diminish in length from above downwards. The anthers open by means of terminal pores. The pod is compressed and broad and flat. The flowers are borne in racemes in the axils of the leaves of the shrub, which is about a metre high. The bright green, equally pinnate leaves have small stipules at the base. *Tamarindus indica* (Fig. 703) is a handsome tree, native to tropical Africa, but now planted throughout the tropics. Its broadly-spreading crown of light foliage makes it a favourite shade-tree. The racemes of flowers are terminal on lateral twigs bearing equally pinnate leaves. The individual flowers are markedly zygomorphic. The fruit is peculiar. The pericarp is differentiated into an outer brittle exocarp, a succulent mesocarp, and a firm endocarp consisting of stone-cells investing the more or less numerous seeds individually (Fig. 704). The almost imperceptibly dorsiventral flowers of *Copaïfera* have no corolla; the four sepals are succeeded by 8-10 free stamens. The fruit is one-seeded but opens when ripe. The seed is invested on one side by a succulent, irregularly-limited arillus. None of the Caesalpiniaceae are British. *Ceratonia siliqua* and the cauliflorous (cf. p. 732) *Cercis siliquastrum* from the Mediterranean region (Fig. 701 *A*) and *Gleditschia triacanthos* (N. Am.) (Fig. 193), are sometimes cultivated as ornamental plants.

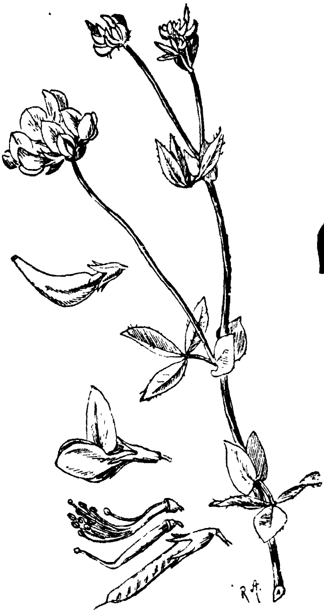


FIG. 707.—*Lotus corniculatus* (½ nat size). Flowering shoot; flower, keel, stamens, carpel (nat. size) Fruit (½ nat. size).

FIG. 708.—*Myroxylon Pereirae*. (⅔ nat. size. After BERG and SCHMIDT.)

OFFICIAL.—SENNAE FOLIA and SENNAE FRUCTUS from *Cassia angustifolia* (Trop.

East Africa and Arabia, cultivated at Tinnevelly in Southern India) and from *C. acutifolia* ; *Cassia Fistula* (Trop. Am.) yields CASSIAE FRUCTUS ; COPAIBA is obtained from *Copaïfera Langsdorfii* and other species ; TAMARINDUS from the succulent mesocarp of *Tamarindus indica* ; HAEMATOXYLI LIGNUM, the heart-wood of *Haematoxylon campechianum* (Trop. Am.) ; KRAMERIAE RADIX from *Krameria triandra*, a shrub growing in the Cordilleras. Flowers atypical ; the sepals brightly coloured within ; the corolla small. Three stamens opening by pores at the summit. Fruit spherical, prickly. Leaves simple, silvery white (Fig. 705). SAPPAN from *Caesalpina sappan*.

Family 3. **Papilionaceae.**— Herbs, shrubs, or trees with, as a rule, imparipinnate leaves Flowers always markedly zygomorphic. Calyx of five sepals. Corolla of five petals, papilionaceous, with descending imbricate aestivation (Fig. 706). Stamens ten ; filaments either all coherent into a tube surrounding the pistil (*Lupinus*) or the posterior stamen is free (*Lotus*), or all are free (*Myroxylon*, Fig. 709). Seeds with a curved embryo.

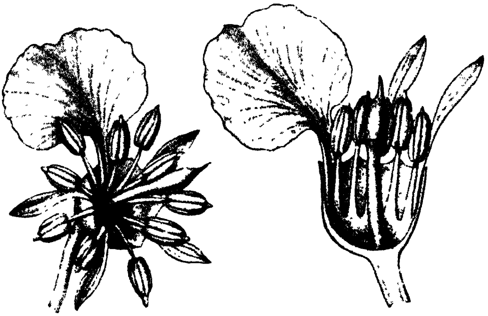


FIG. 709.—*Myroxylon Pereirae*. See Text. (Enlarged. After BERG and SCHMIDT.)

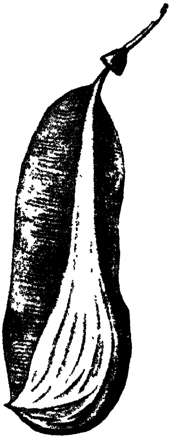


FIG. 710.—Fruit of *Myroxylon Pereirae*. (⅔ nat. size.)

Abundantly represented in the temperate zones ; fewer in the tropics.

The component parts of a papilionaceous flower are seen separately in Fig. 707. The posterior petal, which overlaps the others in the bud (Fig. 706), is termed the standard (vexillum). The two adjoining lateral petals are the wings (alae), and the two lowest petals, usually coherent by their lower margins, together form the keel (carina). The upper ends of the stamens are usually free and curve upwards, as does also the style bearing the stigma.

The genus *Myroxylon* is of importance on account of the balsam obtained from species belonging to it. *Myroxylon Pereirae* is a tree of moderate height with alternate, imparipinnate leaves (Fig. 708). The flowers are borne in terminal racemes and have a large vexillum, the other petals remaining narrow and inconspicuous. The stamens are only coherent at the base, and bear conspicuous, reddish-yellow anthers (Fig. 709). The fruit is very peculiar. The ovary has a long stalk and bears two ovules near the tip. One of these develops into the seed of the indehiscent, compressed pod, which has a broad wing along the ventral suture and a narrower wing along the dorsal suture (Fig. 710). The bell-shaped calyx persists on the stalk. *Genista*, *Sarothamnus*, *Lupinus*, *Cytisus* have all ten stamens united (Fig. 706 *B*); their leaves are pinnate or simple, with entire margins. The Laburnum (*Laburnum vulgare*, Fig. 268) is one of the commonest ornamental trees of our gardens and grows wild in the Alps. It has tripinnate leaves and long pendulous racemes of yellow flowers. *Ulex*, Furze, a characteristic British plant. *Spartium*, distributed in the Mediterranean region. *Trifolium*, Clover, with persistent calyx and corolla. Leaves trifoliate. Flowers aggregated in heads. Stamens (9) + 1. Fruits indehiscent. *Medicago*, Medick, with deciduous corolla; fruit sickle-shaped or spirally twisted. *Melilotus*, Melilot, with racemose inflorescences. *Trigonella* with long pods. *Ononis*, Rest-Harrow, with ten coherent stamens. The increase in the amount of nitrogen in the soil effected by the root-tubercles (cf. Fig. 248) of Leguminosae finds its practical application in European agriculture in the cultivation of species of *Trifolium*, *Medicago*, and *Lupinus*. *Lotus*, Bird's-foot Trefoil (Fig. 707); leaves imparipinnate, lowest pair of leaflets owing to the absence of the petiole resembling stipules. *Anthyllis*, Kidney-Vetch. In species of *Astragalus*, which are low shrubs of the eastern Mediterranean region and of western Asia, the rachis of the leaf persists as a sharply pointed thorn for years after the leaflets have fallen. These spines serve to protect the young shoots, leaves, and flowers (Fig. 711). Our native species are herbaceous. *Robinia* (Fig. 176) is an American tree of rapid growth with very brittle wood, which is often planted and known as False Acacia. *Glycyrrhiza*, Liquorice, is a native of South Europe. *Wistaria sinensis* is a climber with beautiful blue flowers, often grown against the walls of houses. Distinguished by the jointed pods in which the seeds are isolated by transverse septa are *Coronilla*, *Ornithopus sativus*, Bird's-Foot, and *Arachis hypogaea*, Ground-nut, an important, oil-yielding fruit of the tropics and sub-tropics. After flowering the flower-stalks penetrate the soil in which the fruits ripen. *Vicia*, Vetch; *Pisum*, Pea (Fig. 201); *Lens*, Lentil; *Lathyrus*, Everlasting Pea (Fig. 202).

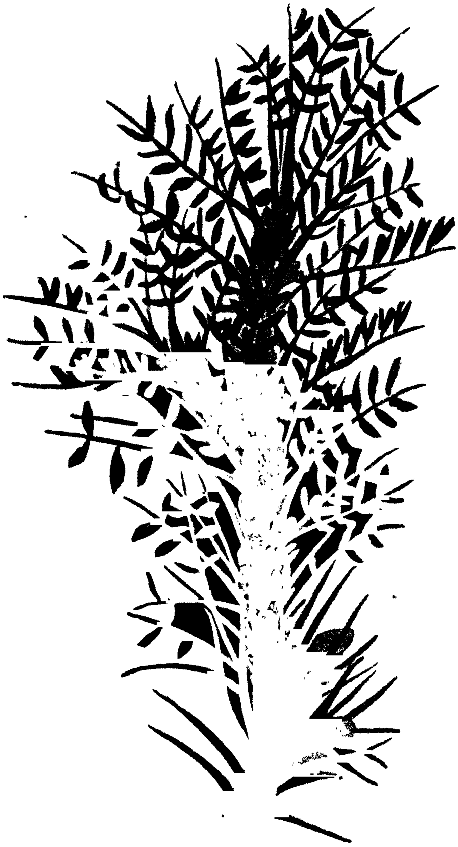


FIG. 711.– *Astragalus gummifer*. (¼ nat. size. After A. MEYER and SCHUMANN.)

Leaves with terminal tendrils, corresponding to the terminal leaflet; the leaves may thus appear to be paripinnate. The cotyledons remain within the seed-coat and do not become green. *Vicia Faba*, the Broad Bean, is an erect plant, without tendrils; the terminal leaflet is reduced to a bristle-shaped stump. *Phaseolus*, Kidney Bean, and *Physostigma* are twining plants with tripinnate leaves. *Physostigma venosum*, a West African climber, yields Calabar Bean.

POISONOUS.—Among our common Leguminosae only *Laburnum vulgare* and the related genus *Cytisus* are extremely poisonous. *Coronilla varia*, with umbels of rose-coloured flowers, and *Wistaria sinensis* are also poisonous.

OFFICIAL.—*Astragalus gummifer* and other species yield TRAGACANTHA. GLYCYRRHIZAE RADIX is obtained from *Glycyrrhiza glabra*. *Spartium scoparium* (*Cytisus scoparius*) yields SCOPARII CACUMINA. *Andira Araroba*, a Brazilian tree, contains a powdery excretion in cavities of the stem called ARAROBA; CHRYSAROBINUM is obtained from this. The heart-wood of *Pterocarpus santalinus*, an East Indian tree, is PTEROCARPI LIGNUM. KINO is obtained from the juice flowing from incisions in the trunk of *Pterocarpus Marsupium*. *Myroxylon toluifera* (South America) yields BALSAMUM TOLUTANUM, and *M. Pereirae* (San Salvador) BALSAMUM PERUVIANUM. *Arachis hypogaea* yields OLEUM ARACHIS. *Butea frondosa* yields BUTEAE SEMINA. *Physostigma venenosum* yields PHYSOSTIGMINE.

Order 15. Myrtales

This order differs from the Rosiflorae by the inferior ovary, the prevalence of tetramery, and the absence of stipules.

Family 1. **Thymelaeaceae.**—Ovule pendulous. *Daphne Mezereum* (Fig. 712) is a poisonous shrub, possibly native to Britain, which flowers in February and March before the leaves appear. The flowers are rose-coloured, scented, tetramerous, and have no corolla. The leaves form a close tuft until the axis elongates. The fruit is a bright red berry. In the Alps and in the Mediterranean region there are several species of *Daphne*, all of which are poisonous.

Family 2. **Elaeagnaceae.**—Ovule erect. *Hippophaë*. *Elaeagnus*. The leaves and young twigs are covered with shining peltate hairs. *Shepherdia* (Fig. 52) is similar.

Family 3. **Lythraceae.**—*Lythrum salicaria*. Purple Loosestrife. Flowers typically hexamerous with two to six carpels. Heterostyled with three forms of flower (cf. p. 571).

Family 4. **Onagraceae.**—Flower tetramerous throughout. Androecium obdiplostemonous. *Epilobium*, Willow-herb, with numerous species; the fruit is a capsule, and the seeds have hairs serving for wind-dispersal. *Oenothera* (Fig. 713). The power of mutating possessed by plants of this genus was recognised by DE VRIES (39) and forms the experimental basis of his hypothesis of mutation. *Circaea*, Enchanter's Nightshade. *Trapa*, Water Nut. Many forms are in cultivation, for instance the species of *Fuchsia*, in which the calyx is petaloid. These plants are natives of America. Fruit, a berry.

Family 5. **Rhizophoraceae** (38a).—Plants occurring in the Mangrove formation along tropical coasts, characterised by vivipary and the possession of stilt-roots, or respiratory roots (Fig. 182). These adaptations are related to the peculiarities of the situations in which the trees grow. *Rhizophora* (Fig. 715); *Bruguiera*; *Ceriops*. *Kandelia*. All occur on the coasts of the Indian Ocean. Species of *Rhizophora* are more widely distributed on tropical coasts.

Family 6. **Myrtaceae.**—Evergreen shrubs or trees; leaves opposite, leathery, often aromatic. Flowers actinomorphic, tetramerous or pentamerous. Androecium of many stamens, which are often arranged in bundles which have originated by branching. Carpels two or many (Fig. 714) united with the floral axis to form the inferior ovary. Fruit, usually a berry or a capsule.

Mainly distributed in tropical America and in Australia.

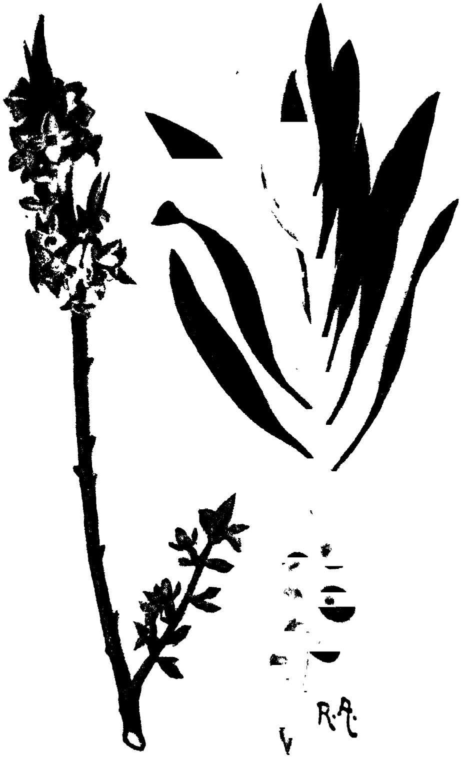


Fig. 712.—*Daphne Mezereum* (½ nat. size). *Poisonous.*

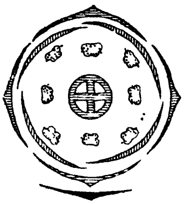


Fig. 713.—Floral diagram of *Oenothera* (Onagraceae). After Noll.

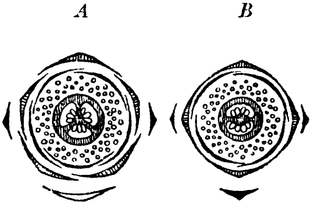


Fig. 714.—Floral diagrams of Myrtaceae. *A*, *Myrtus communis*. *B*, *Eugenia aromatica*. (After Eichler.)

The Myrtle (*Myrtus communis*), which occurs in the Mediterranean region, is the only European species. Species of *Eucalyptus* (^{38}) from Australia, especially *E. globulus*, are commonly planted in warm climates, on account of their rapid growth and useful timber. Young plants have opposite, sessile leaves, but older trees bear stalked, sickle-shaped leaves which hang vertically. *E. amygdalina*, which reaches a height of 150 m. and a circumference of 30 m. at the base of the trunk, is one of the largest forest trees known. *Psidium guayava* and some species of *Jambosa* bear edible fruits; the former is especially valued. *Jambosa caryophyllus* (Moluccas) is of economic importance, its unopened flower-buds forming Cloves (Fig. 716). This tree is commonly cultivated in the tropics. In Fig. 716 the inferior ovary, formed of two carpels, is also seen in longitudinal section. Species of *Sonneratia* are frequently the constituents of the mangrove vegetation that advance farthest into the sea; their pneumatophores therefore attain a considerable height (Fig. 181).

OFFICIAL.—*Eugenia Caryophyllata* yields CARYOPHYLLUM, Cloves. OLEUM CAJUPUTI from *Melaleuca Leucadendron*, a tree of less height but resembling the Eucalyptus trees; it is cultivated in the Moluccas (Buru) for the sake of the oil it yields; its specific name refers to the white colour of the bark. OLEUM EUCALYPTI and KINO EUCALYPTI from *Eucalyptus globulus* and other species.

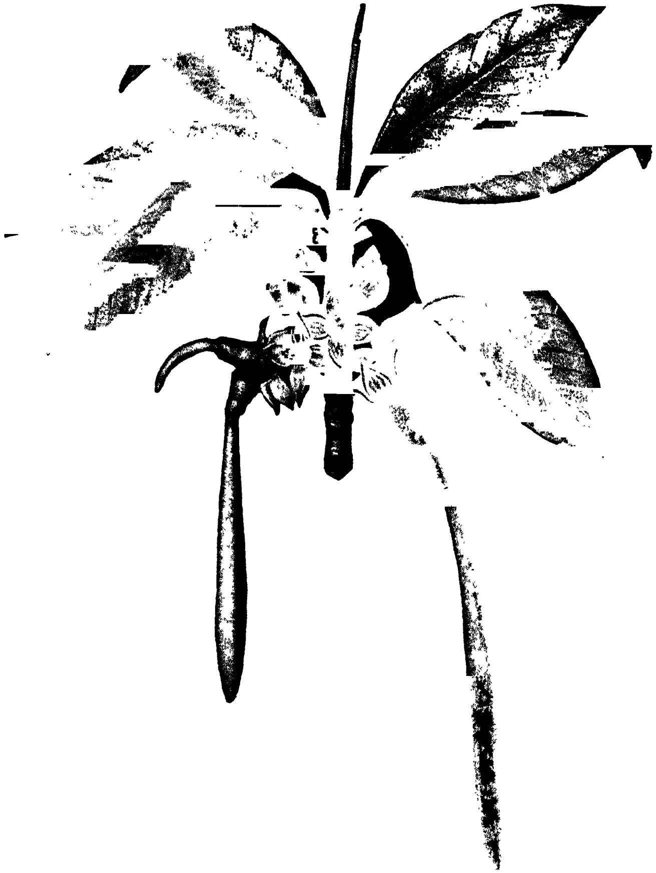


FIG. 715.—*Rhizophora conjugata* (½ nat. size)

Family 7. **Punicaceae.**—Single genus *Punica*. *Punica granatum* is a tree originally introduced from the East and now largely cultivated in the Mediterranean region on account of its acid refreshing fruits known as Pomegranates (Fig. 717). Leaves small, entire. Flower with a stiff, red calyx, an indefinite number of petals, and numerous stamens; the 7-14 carpels are arranged in two tiers, the upper of which corresponds in number to the sepals, the lower to the half of this (Figs. 717, 2, 718). Fruit enclosed by a leathery pericarp with numerous seeds in the loculi of both tiers. The external layers of the seed-coat become succulent and form the edible portion of the fruit.

Order 16. Euphorbiales (Tricoccae) (40)

This order is placed here, after the preceding description of the orders which can be directly connected with the Polycarpicae, since the Euphorbiales can be regarded as a similar though less far-reaching initial group. Whether or in what degree the Euphorbiales are connected with the Polycarpicae is a difficult question. It appears rather as if such special features as those of the cyathium (Fig. 721) might be traced back to Gymnosperm inflorescences. When the stamens, which each correspond to a male flower, have an articulation between the filament and the stalk, or in some cases (*Anthostema*, etc.) exhibit a well-formed perianth in this position, the distinction from the condition in *Gnetum* or *Ephedra* is not so great. It is true that it is not possible to trace similar analogies in the case of the female flowers.

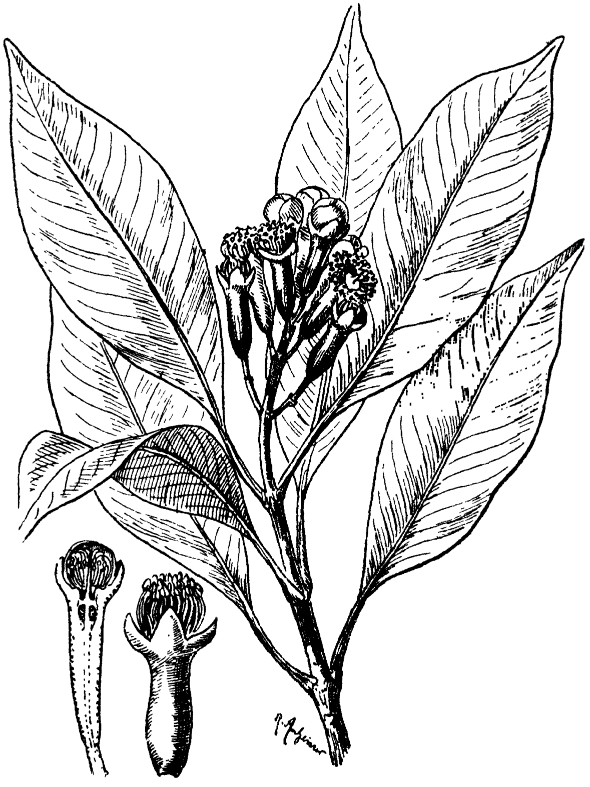


FIG. 716.—*Eugenia caryophyllata* (⅔ nat. size). Flowering branch. A bud cut in half and an opened flower (about nat. size).

On the other hand, there is no doubt as to the cyathium being an inflorescence, and in this respect also there would seem to be an approach to Gymnosperm ancestors. It is further to be considered that hermaphrodite flowers are also wanting in the forms which do not possess cyathia, and that the distribution of the flowers may be either monoecious or dioecious.

In the other direction the Euphorbiaceae exhibit affinities, especially to the Malvaceae, Geraniaceae, Linaceae, Polygalaceae, and Aceraceae: they agree in the structure of the ovary, the loculi of which, as in the Euphorbiaceae, contain only one or two ovules. Possibly also some significance may be attached to the possession of stipules. Thus it would appear, and this is confirmed serologically, that the Columniferae and Gruinales are to be regarded as the most nearly related orders.

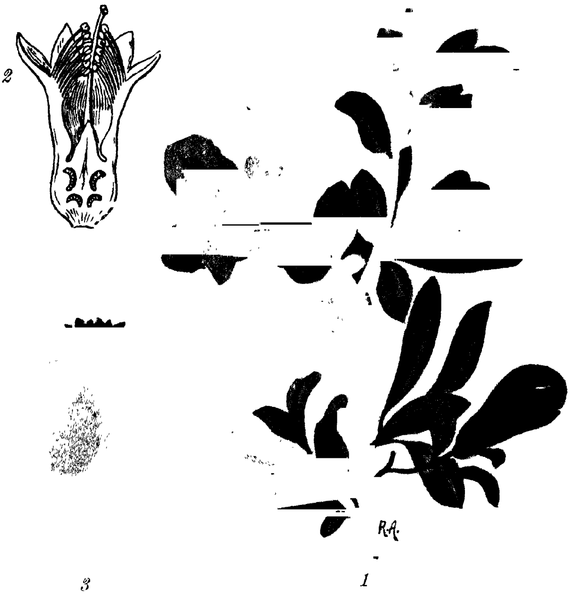


FIG. 717.—*Punica granatum* (½ nat. size). 1, Branch bearing a flower and a bud. 2, Flower in longitudinal section. 3, Fruit. (See text.)

Family **Euphorbiaceae.**—The plants belonging to the Euphorbiaceae are of very diverse habit. The order includes herbs, shrubs, leafless succulent plants, trees with normal foliage, and others with scale-leaves and assimilating phylloclades. The plants agree, however, in possessing unisexual, actinomorphic flowers, with a simple perianth or with no trace of the latter. Androecium diplostemonous, or stamens numerous. The female flowers are especially characterised by the superior, trilocular ovary formed of three carpels; in each loculus are one or two pendulous ovules with a ventral raphe, and the micropyle directed upwards and outwards.

The micropyle is covered by a placental outgrowth called the OBTURATOR (Fig. 719); this assists in conducting and nourishing the pollen-tube, and disappears after fertilisation (cf. p. 587). The CARUNCULA, which is formed from the outer integument (Fig. 721 *D*), persists on the other hand in the seed; the separation of the latter from the placenta is assisted by it. The fruit is a capsule, the outer walls of which contract elastically away from a central column, and thus open the loculi.

The plants of this family are distributed over the whole earth. IMPORTANT GENERA.—Many Euphorbiaceae are dioecious or monoecious, and have flowers of relatively simple construction. Thus *Mercurialis* (Fig. 720), two species of which occur in Britain, is characterised by its bicarpellary ovary. *Croton* is a tropical genus including valuable official plants, *C. Eleuteria* and *C. Tiglium*; the male flowers have a double, the female flowers a single perianth. In the Spurges (*Euphorbia*), of which there are several British species, a number of the extremely simply constructed flowers are grouped in a complicated inflorescence termed a CYATHIUM (Figs. 721-23), which, especially when zygomorphic as in *Pedilanthus*, gives the impression of a single flower. The cyathium consists of a naked, terminal, female flower, borne on a long bent stalk surrounded by a number of groups of male flowers. Each of the latter is stalked and consists of a single stamen, the limit between which and the flower-stalk is distinguishable. In some cases the female flower and each male flower are provided with a small perianth. The whole cyathium, which is an inflorescence, is always enclosed by five involucral bracts; alternating with these are four nectar-secreting glands, the presence of which increases the likeness between the cyathium and a flower. The fifth gland is wanting, and the inverted female flower hangs down in the gap thus left. Between the groups of male flowers which stand opposite to the bracts

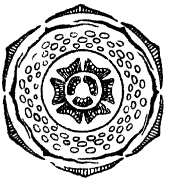


FIG. 718.—Floral diagram of *Punica granatum*. (After EICHLER.)

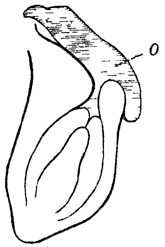


FIG. 719.—Ovule of *Euphorbia dioica* showing the obturator o. (After PAX in ENGLER-PRANTL.)

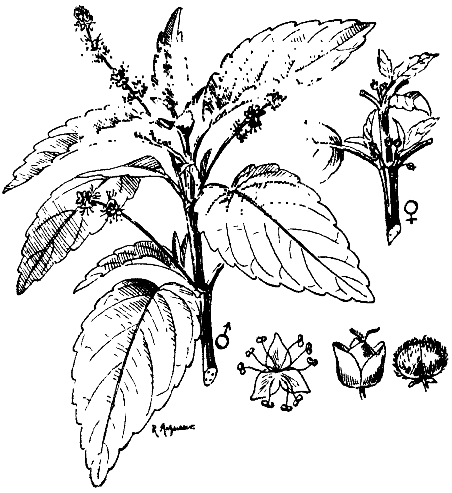


FIG. 720.—*Mercurialis annua* (½ nat. size). Male plant in flower and single male flower. Portion of a female plant single female flower and fruit. *POISONOUS.*

(Fig. 721) are branched hairs which are visible when the cyathium is cut through

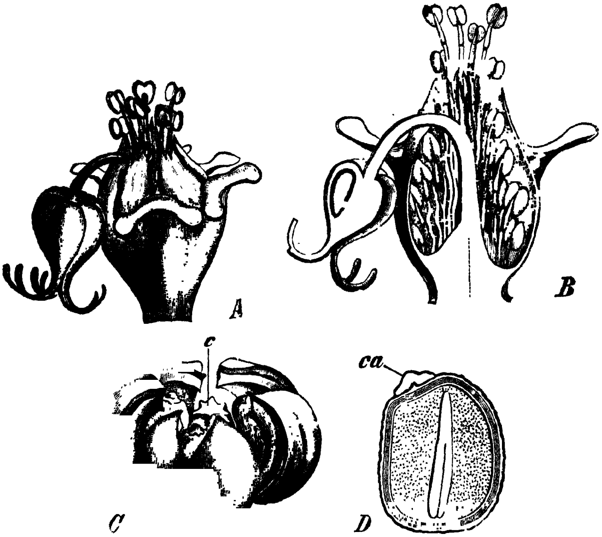


FIG. 721.—*Euphorbia Lathyris.* *A*, Cyathium (× 4). *B*, Cyathium cut through longitudinally (× 7). *C*, Fruit after dehiscence showing the central column (*c*). *D*, Seed in longitudinal section showing the embryo embedded in the endosperm; *ca*, caruncula (× 4). (*A-D* after BAILLON.)

longitudinally (Fig. 721 *B*). The cyathia are usually grouped in dichasia, and these in turn form an umbellate inflorescence, with three to many branches. It often happens that the female flower is only developed in some of the cyathia, remaining rudimentary in the others. Many species of *Euphorbia*, especially the African species, are succulent-stemmed plants resembling *Cacti* in general appearance (Fig. 723).

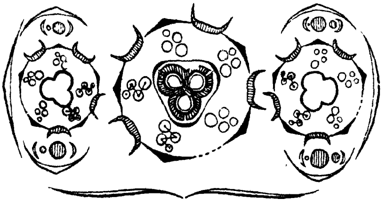


FIG. 722.—Diagram of a dichasial branch of *Euphorbia*, with three cyathia, only the middle one of which has a fertile female flower. (After EICHLER.)

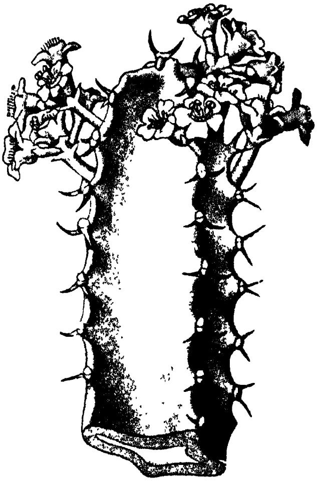


FIG. 723.—*Euphorbia resinifera* (nat. size). (After BERG and SCHMIDT.)

Euphorbia, like many but not all the other plants of the family, contains a milky juice, which is secreted in non-septate latex-tubes (sometimes septate, e.g. *Hevea*). This juice, which in many cases is poisonous, exudes wherever the plant is wounded.

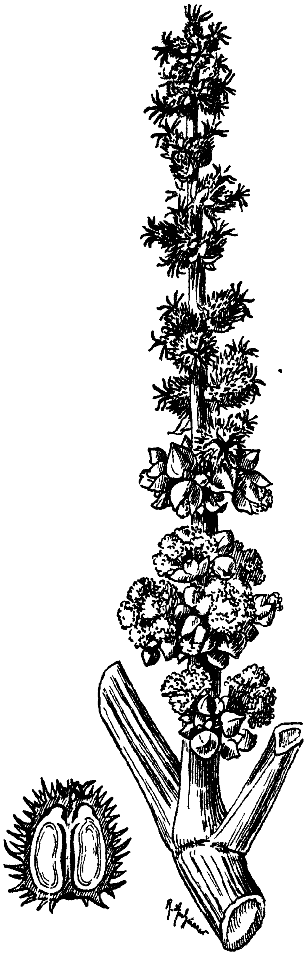


FIG. 724.—*Ricinus communis.* Inflorescence (½ nat. size); young fruit cut through longitudinally.

An important constituent of the latex of species of *Hevea* is CAOUTCHOUC (cf. [32], [48]). As Para Rubber, obtained in the tropics of South America, especially in the Amazon Region, this for long provided about one-half of the total rubber supply. Now, however, the main supply of rubber comes from plantations of *Hevea*, *Ficus*, and *Castilloa*, in the tropical colonies of other regions. In addition, *Manihot Glaziovii*, another South American plant of this order, which yields Ceara Rubber, must be mentioned. A nearly related plant, *Manihot utilissima*, provides in its tuberous roots a very important food in the tropics. The starch obtained from these roots forms mandioc or cassava meal, the finest varieties of which, as tapioca or Brazilian arrowroot, are of commercial importance. The shrub, which is a native of Brazil, is now cultivated throughout the tropics.

Ricinus communis is a tall shrub of tropical Africa. In our climate it is annually killed by the frost. The hollow stem bears large palmately divided leaves. The terminal inflorescences (**Fig.** 724) are overtopped by vegetative lateral branches. The male flowers, situated towards the base, have a membranous calyx of 4-5 sepals, enclosing the branched stamens; the end of each branch bears a theca. The female flowers, nearer the summit of the inflorescence, have 3-5 sepals and a large tripartite ovary. The latter is covered with warty prickles, and bears three large, bifid, red stigmas In each loculus of the fruit is a mottled seed with a whitish caruncula.

OFFICIAL.—*Croton Eleuteria* (Bahamas) yields CASCARILLA. *C. Tiglium* (East Indies), OLEUM CROTONIS. OLEUM RICINI, Castor Oil, is obtained from *Ricinus communis*.

Order 17. Columniferae

The plants of this order possess pentamerous, actinomorphic, hermaphrodite flowers. One of the two whorls of stamens, usually the outer one, is suppressed or only represented by staminodes, while the other whorl has undergone a greater or less increase in the number of its members by chorisis. The branching is frequently accompanied by cohesion of the filaments. The carpels also sometimes exhibit an increase in number as a result of branching. The superior ovary is then divided into a corresponding number of loculi.

Family 1. **Malvaceae.**—Characterised by the flowers with the corolla contorted in the bud. Protandrous. Stamens united into an epipetalous tube around the ovary; the free ends of the stamens, each of which bears a single reniform theca, project from the margin of the staminal tube. K 5, C 5, A ∞, $\underline{G}$ (3) or ∞. Pollen-grains with spiny exine, so that they readily adhere to the hairy bodies of insects (Fig. 538).

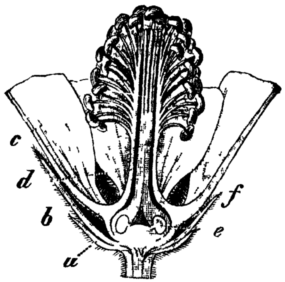


Fig. 725.—Flower of *Althaea officinalis*, cut through longitudinally; parts of the petals are removed. *a*, Outer; *b*, inner calyx; *c*, petals; *d*, androecium; *f*, pistil; *e*, ovule. (After Berg and Schmidt.)

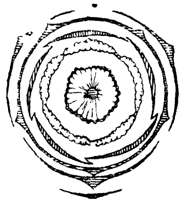


Fig. 726.—Malvaceae. Floral diagram (*Malva*).

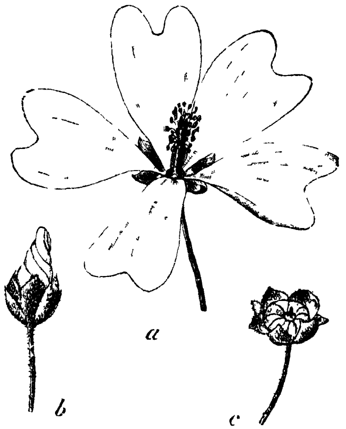


Fig. 727.—*Malva sylvestris.* *a*, Flower; *b*, flower-bud; *c*, fruit. (Nat. size.)

The genus *Malva*, which occurs in Britain, includes perennial herbs, with long-stalked, palmately-veined leaves. Flowers solitary or in small cymose inflorescences, in the axils of leaves. Three free segments of the epicalyx. Petals usually rose-coloured, deeply notched (Fig. 727). In *Althaea* the whole plant is clothed with stellate hairs, giving it a soft, velvety appearance. Epicalyx of 6-9 segments united at the base. The fruit is a schizocarp consisting of numerous carpels arranged in a whorl.

Hibiscus and *Gossypium* are shrubs or trees with three- to five-lobed leaves with long stalks. Flowers with a large epicalyx of three segments, which completely covers the calyx. Fruit of three to five carpels, loculicidal. Seed of *Gossypium* covered with long hairs which aid in its dispersion by the wind. When stripped from the seeds and cleaned these hairs form cotton wool. The most important species of Cotton are *G barbadense*, *G. arboreum*, *G. herbaceum* (Fig. 728).

OFFICIAL — *Gossypium herbaceum* and other species yield GOSSYPIUM and GOSSYPII RADICIS CORTEX.

Family 2. Tiliaceae. — Plants with simple, stalked leaves provided with deciduous stipules Calyx polysepalous Aestivation of calyx and corolla valvate.

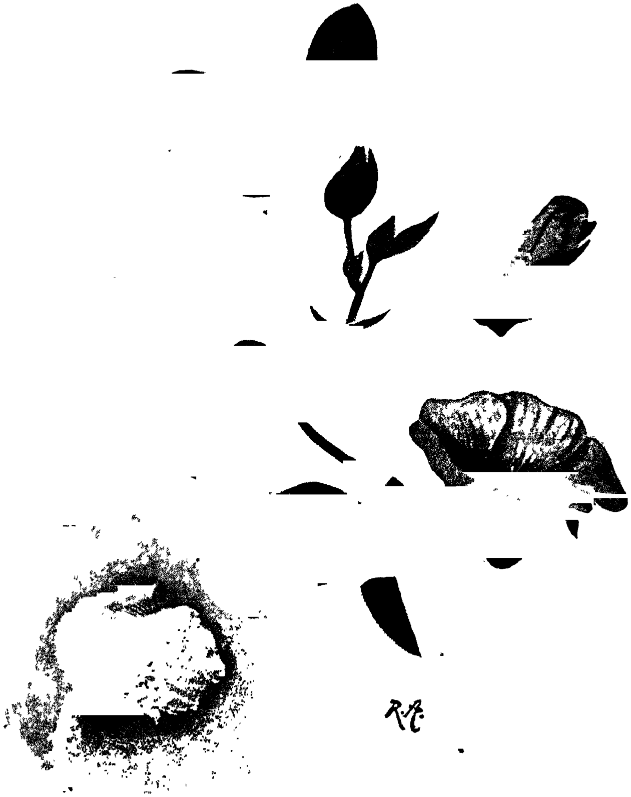


FIG 728 — Flowering branch and open fruit of *Gossypium herbaceum* (½ nat size)

Stamens completely free from one another with introrse anthers ; usually only the inner whorl is present and has undergone branching (Fig 729). Style simple.

Most of the genera are tropical The herbaceous species of *Corchorus* yield Jute. In Britain two species of *Tilia*, Lime, occur These are stately trees with two-ranked petiolate leaves, the stipules of which are soon shed. The leaves, which have a serrate margin, are asymmetrical. The inflorescence (Fig. 731 *A*) is coherent with a bract for half its length , this serves as a wing in the distribution of the fruit. The umbel-like inflorescence of the Lime is composed of dichasia; *Tilia platyphyllos* has 3-7, *T. parvifolia* 11 or more flowers in the inflorescence. The hairy ovary has two ovules in each of its five loculi. The fruit only contains one seed (Fig. 731 *B*).

Family 3. **Sterculiaceae.**—This family, which is distributed in the tropics, resembles the Tiliaceae. Flowers with a gamosepalous calyx; corolla twisted in the bud; stamens coherent to form a tube. The antisepalous stamens are staminodial; the antipetalous stamens are often increased in number (Fig. 730). Anther extrorse.

The most important plant is the Cocoa tree (*Theobroma Cacao*, Fig. 732). It is a native of tropical Central and South America, but has long been cultivated. It is a low tree with short-stalked, firm, brittle, simple leaves of large size, oval shape, and dark green colour. The young leaves are of a bright red colour, and, as in many tropical trees, hang limply downwards. The flowers are borne on the main stem or the older branches, and arise from dormant axillary buds (CAULIFLORY). Each petal is bulged out at the base, narrows considerably above this, and ends in an expanded tip. The form of the reddish flowers is thus somewhat urn-shaped with five radiating points. The pentalocular ovary has numerous ovules in each loculus. As the fruit develops, the soft tissue of the septa extends between the single seeds; the ripe fruit is thus unilocular and many-seeded. The seed-coat is filled by the embryo, which has two large, folded, brittle cotyledons. *Cola acuminata* and *C. vera*, natives of tropical Africa, yield the Kola nuts which are used in medicine.

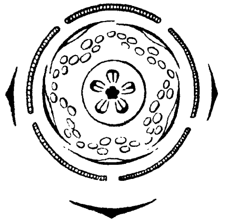


FIG. 729.—Tiliaceae. Floral diagram (*Tilia*). (After EICHLER.)

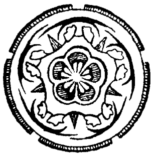


FIG. 730.—Sterculiaceae. Floral diagram (*Theobroma*). (After EICHLER.)

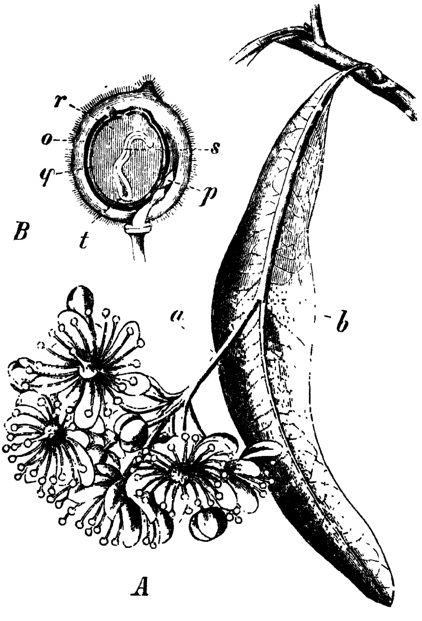


FIG. 731.—*Tilia ulmifolia*. *A*, Inflorescence (*a*), with bract (*b*), (nat. size). *B*, Longitudinal section of fruit (magnified); *o*, pericarp; *p*, atrophied dissepiment and ovules; *q*, seed; *r*, endosperm; *s*, embryo; *t*, its radicle. (After BERG and SCHMIDT.)

OFFICIAL.—OLEUM THEOBROMATIS is obtained from *Theobroma Cacao*.

Order 18. Gruinales

The flowers of the majority of the plants belonging to this order are hermaphrodite, pentamerous, and radially symmetrical, with a superior, septate ovary. K 5, C 5, A 5 + 5, G (5). When the flowers are zygomorphic they frequently exhibit reduction (Polygalaceae). Stamens coherent at the base, obdiplostemonous or haplostemonous. Nectaries to the outer side of the stamens or as an annular disc,

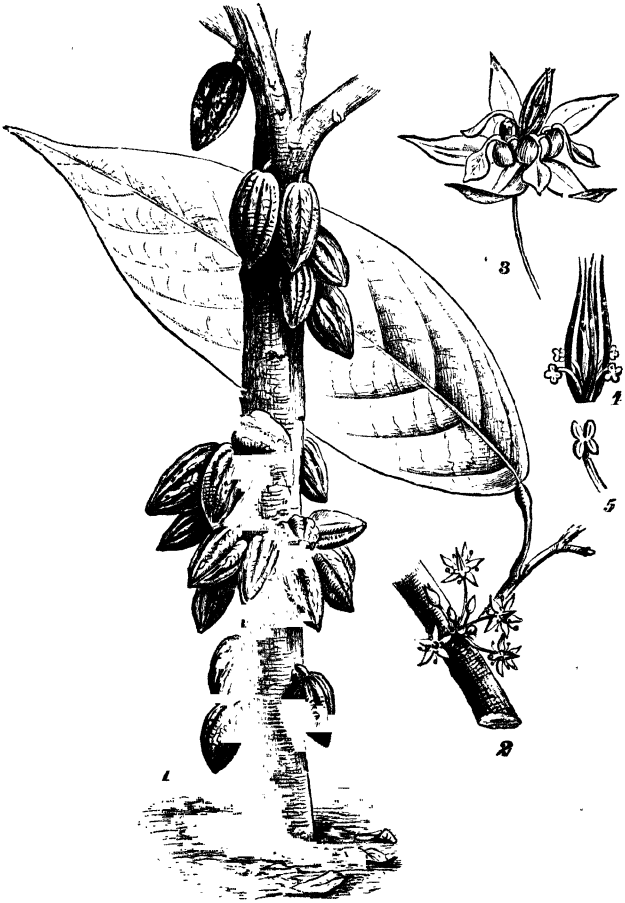


FIG. 782.—*Theobroma Cacao.* *1*, Stem bearing fruits. *2*, Flowering branch. *3*, Flower. *4*, Circle of stamens. *5*, Stamen from anterior side. (*3*, *4*, about nat. size: *5*, enlarged; *1*, *2*, greatly reduced.)

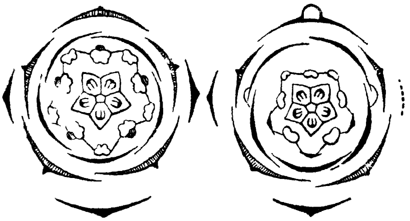
within the stamens (Rutaceae). Ovules usually pendulous, with the micropyle directed upwards and the raphe ventral; or the micropyle is downwardly directed and the raphe dorsal.

Family 1. **Geraniaceae.**—The genera *Geranium* (Fig. 733) with actinomorphic and *Pelargonium* (Fig. 734) with dorsiventral flowers both have stalked, palmately-veined leaves. *Erodium* (40a). Two ovules in each loculus. When ripe the five beaked carpels separate from a central column, and either open to liberate the seeds, or remain closed and by the hygroscopic movements of the awn-like portion bury the seed in the soil (Fig. 735 ; cf. Fig. 276, p. 336).

Family 2. **Linaceae.**—*Linum usitatissimum*, Flax (Fig. 737), has long been in cultivation. It is an annual, and bears numerous blue flowers, which last only a short time, in racemose cincinni. The flower has its stamens united at the base and five free styles. The stem bears numerous small narrow leaves. The bast-fibres after proper preparation are woven into linen. The seeds from the 5-locular capsule yield oil, and are also official on account of their mucilaginous epidermis.

OFFICIAL.—LINI SEMINA, the seeds of *Linum usitatissimum*.

Family 3. **Erythroxylaceae.**—OFFICIAL.—*Erythroxylon Coca* is a small Peruvian shrub, with entire, simple leaves and axillary groups of small white flowers (Fig. 736). COCAINA is obtained from the leaves of this plant.



Floral diagrams of Geraniaceae.

FIG. 733.—*Geranium pratense*. (After EICHLER.) FIG. 734.—*Pelargonium zonale*. (After EICHLER.)

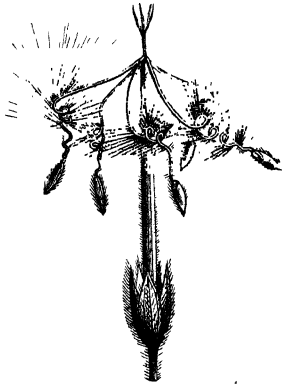


FIG. 735.—Fruit of *Pelargonium inquinans*. (× 3. After BAILLON.)

Family 4. **Zygophyllaceae.**

OFFICIAL.—*Guiacum sanctum* and *Guiacum officinale*, West Indian trees with opposite, paripinnate leaves. They yield GUIACI LIGNUM and GUIACI RESINA.

Family 5. **Rutaceae.**—IMPORTANT GENERA.—*Ruta graveolens* (Fig. 738), the Rue, is a somewhat shrubby plant with pinnately-divided leaves. The terminal flowers of the dichasial inflorescences are pentamerous in robust examples; all the other flowers are tetramerous with a large intrastaminal disc. *Dictamnus Fraxinella* has panicles of conspicuous, dorsiventral flowers ; the carpels are free in their upper portions. The important genus *Citrus* (41) has peculiarly constructed flowers (Figs. 739, 740). The numerous stamens are united in bundles and arranged in a single whorl. The number of carpels is also increased. The fruit is a berry ; the succulent portion is formed of large cells with abundant cell-sap which project into and fill up the loculi of the ovary. The seeds have usually several embryos (cf. p. 590). The leaves of many species are simple and provided with more or less winged petioles. Other species have trifoliate leaves, and the articulation at the base of the lamina shows that the apparently simple leaves correspond to imparipinnate leaves, of which only the terminal leaflet is developed. The thorns at the base of the leaf are derived by modification of the first leaves of the axillary bud. *Citrus* is originally an East Asiatic genus; a number of species inhabit the warmer valleys of the Himalayas. All the important cultivated forms have been obtained from the Chinese. *Citrus decumana*, the Shaddock, is tropical; *C. medica* is the form which was known to the Greeks in the expeditions of Alexander as the Median apple. It is now widely spread and has a number of varieties of which *Citrus* (*medica*) *Limonum* is the Lemon. This tree was introduced into the Mediterranean region in the third or fourth century. *Citrus* (*medica*) *Bajoura* has thick-skinned fruits from which citron is obtained. *Citrus Aurantium* occurs in two distinct forms, *C.* (*Aurantium*) *vulgaris* (Fig. 740) and *C.* (*Aurantium*) *sinensis*. *Citrus nobilis*, the Mandarin, is also of Chinese origin. Chimaeras, called *Bizzaria*, have been obtained by grafting between *Citrus Aurantium* and *C. Limonum*. *Pilocarpus pennatifolius* and *P. jaborandi*, tree-like shrubs with large, imparipinnate leaves, natives of Eastern Brazil.

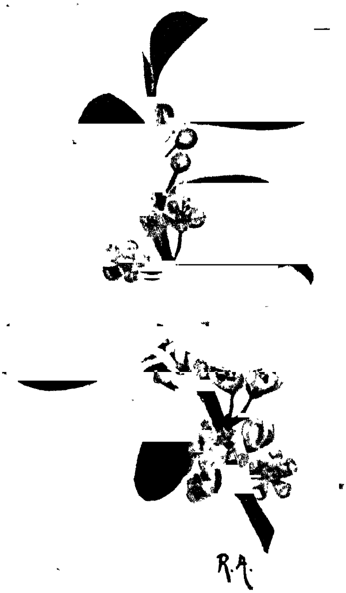


FIG. 736.—*Erythroxylon Coca.* (⅔ nat. size.)

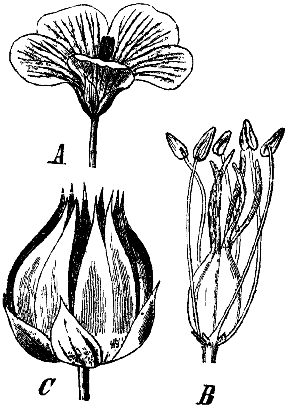


FIG. 737.—*Linum usitatissimum.* *A*, Flower. *B*, Androecium and gynaeceum. *C*, Capsule after dehiscence. (*A*, nat. size; *B*, *C* × 3.)

OFFICIAL.—*Citrus Aurantium*, var. *Bigaradia*, yields AURANTII CORTEX SICCATUS, AURANTII CORTEX RECENS, and AQUA AURANTII FLORIS. *Citrus medica*, var. *limonum*, gives LIMONIS CORTEX, OLEUM LIMONIS, and LIMONIS SUCCUS. *Aegle Marmelos* yields BELAE FRUCTUS. BUCHU FOLIA are obtained from *Barosma betulina*. *Pilocarpus microphyllus* and *Pilocarpus* sp. yield PILOCARPINAE NITRAS.

Family 6. **Simarubaceae.**—Contain bitter principles. *Quassia amara* (Surinam) (Fig. 741), a small tree with beautiful leaves and showy flowers.

OFFICIAL.—QUASSIAE LIGNUM from *Picraena excelsa* (West Indies).

Family 7. **Burseraceae.** — Woody plants with resin passages. *Commiphora abyssinica* and *C. Schimperi* are trees found in Arabian East Africa. *Boswellia Carteri* and *B. Bhau Dajianae* are small trees from the same region which yield OLIBANUM. *Canarium.*

OFFICIAL.—MYRRHA, Myrrh, from *Commiphora Myrrha* and other species.

Family 8. **Polygalaceae.**—K 5, C 3, A (8), G (2). The two lateral sepals are petaloid. Three petals, the lowest of which forms a keel. Stamens eight, coherent into a tube (Figs. 742-744). *Polygala chamaebuxus* is a small shrubby plant occurring in the Alps. *P. vulgaris* and *P. amara* occur in Britain.

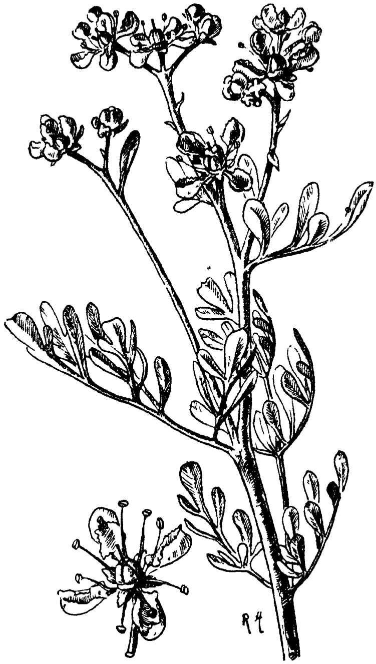


FIG. 738.—*Ruta graveolens*. (½ nat. size.)

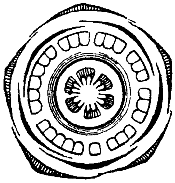


FIG. 739—Floral diagram of *Citrus vulgaris*. (After EICHLER.)

OFFICIAL. — *Polygala Senega* (North America) yields SENEGAE RADIX.

Family 9. **Sapindaceae.** —Tropical. — The crushed seeds of *Paullinia cupana*, a liane of Brazil, yield CAFFEINA.

Family 10. **Anacardiaceae.** —Mostly tropical. *Mangifera indica*; *Rhus toxicodendron*; *Pistacia.*

Family 11. **Aquifoliaceae.** —*Ilex aquifolium.* The

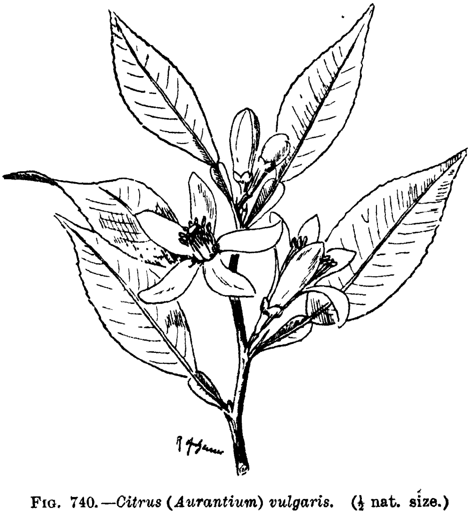


FIG. 740.—*Citrus* (*Aurantium*) *vulgaris*. (½ nat. size.)

Holly, an evergreen shrub or tree of Western Europe (Fig. 745). *I. paraguariensis* yields Paraguay Tea or Maté.

Family 12. **Aceraceae.**—Include Maples and Sycamores with their characteristically winged fruits (Fig. 746).

FIG. 741.—*Quassia amara* (Nat. size. After BERG and SCHMIDT.)

Family 13. **Hippocastanaceae.** —The Horse-chestnut. *Aesculus hippocastanum.*
Family 14 **Celastraceae.**
OFFICIAL.—*Euonymus Atropurpureus* yields EUONYMI CORTEX.

Order 19. Rhamnales

This order is characterised by the single whorl of antipetalous stamens and the intrastaminal disc.

Family 1. **Rhamnaceae.**—The only native genus of this family, which is distributed in the tropics, is *Rhamnus*.

Rh. Frangula (Figs. 747 *B*, 748, 749), the Berry-bearing Alder, is a shrub with alternate, entire leaves provided with small stipules. The flowers are solitary or in groups in the axils of the leaves; pentamerous, with two or three carpels. The floral receptacle forms a cup-shaped disc. Two (less commonly three) carpels; stigma undivided. Fruit, a drupe with two or three seeds. *Rh. cathartica* has usually spiny branches bearing opposite leaves with serrate margins. Flowers tetramerous throughout (Fig. 747 *A*), dioecious by suppression of stamens or carpels; female flower with four free styles and a four-seeded drupe. Seeds with

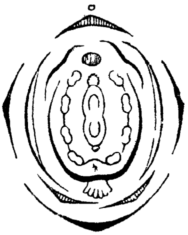


Fig. 742.—Floral diagram of *Polygala myrtifolia*. (After Eichler.)

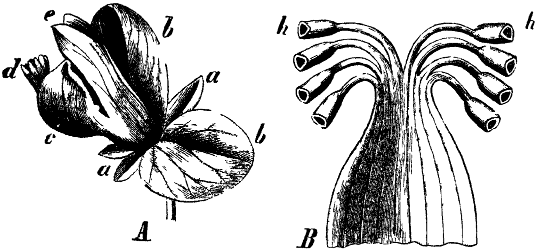


Fig. 743.—*Polygala Senega*. *A*, Flower; *a*, small, *b*, large sepals; *c*, keel, *e*, lateral petals, *d*, androecium. *B*, Androecium; *h*, anthers (magnified). (After Berg and Schmidt.)

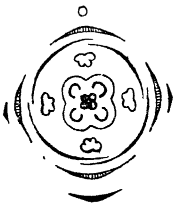


Fig. 745.—Floral diagram of *Ilex aquifolium*. (After Eichler.)

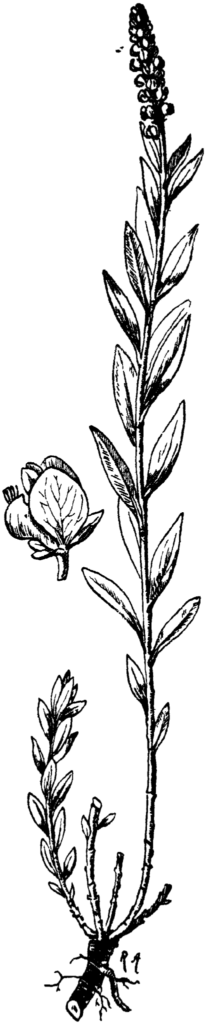


Fig. 744.—*Polygala Senega*. (½ nat. size.)

a dorsal raphe. *Colletia spinosa* and *C. cruciata* are xeromorphic, leafless South American shrubs.

OFFICIAL.—*Rhamnus Purshianus* yields CASCARA SAGRADA or RHAMNI PURSHIANI CORTEX.

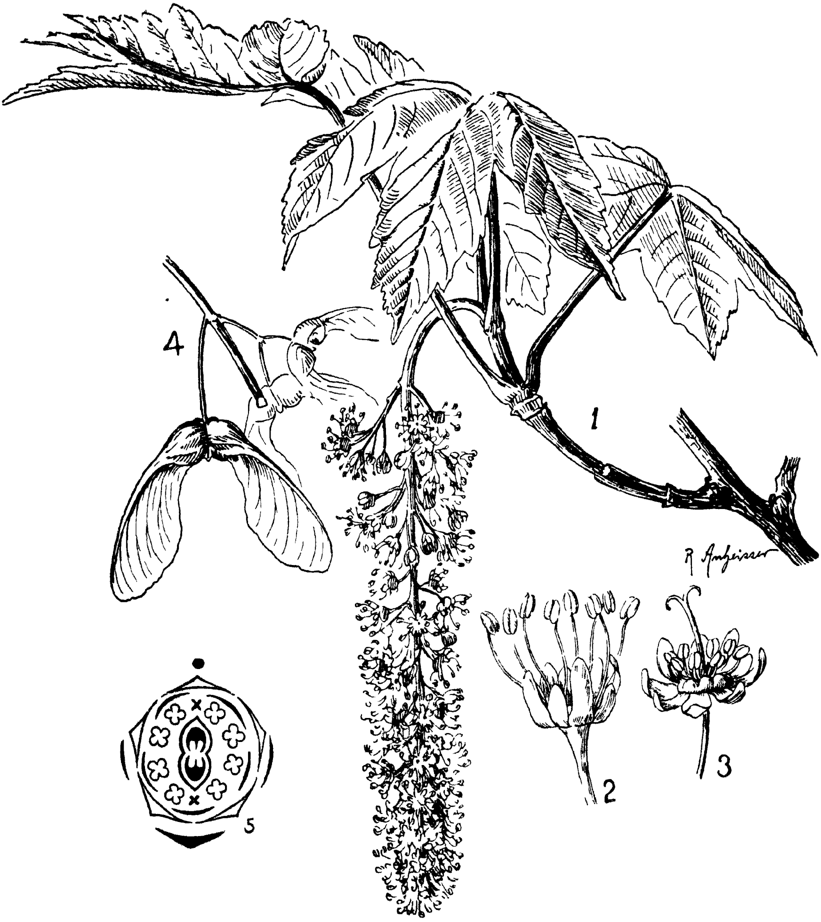


FIG. 746.—*Acer pseudoplatanus* (½ nat. size). *1*, Branch with pendulous terminal inflorescence. *2*, Male flower. *3*, Female flower. *4*, Fruit *5*, Floral diagram. (*2* and *3* enlarged.) (After EICHLER.)

Family 2. **Vitaceae** (Figs. 750, 751).—The genera *Vitis* (^{41a}), *Ampelopsis*, and *Parthenocissus* in the northern hemisphere and the tropical genus *Cissus* belong here. *Vitis vinifera*, the Grape Vine, is a cultivated plant with numerous races and varieties. The tendrils correspond to shoots and stand opposite to the leaves; they are at first terminal, but become displaced to one side by the development of the axillary shoot. The inflorescence is a panicle taking the place of a tendril; intermediate forms between inflorescences and tendrils are of frequent occurrence. Calyx only represented by a small rim; the pentamerous corolla, with the petals united by their tips, is thrown off when the flower opens. Raisins are obtained from *Vitis vinifera.* Currants are the seedless fruits of *Vitis vinifera,* var. *apyrena.* Species of *Parthenocissus* distributed in North America and Asia go by the name of Wild Vines; some of them have tendrils with adhesive discs (Fig. 203).

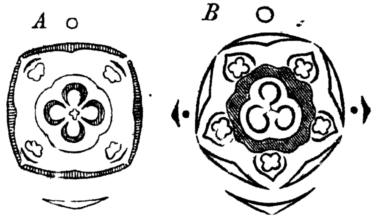


FIG. 747.—Floral diagrams of *A*, *Rhamnus cathartica* (represented as hermaphrodite), and *B*, *Rh. Frangula.* (After EICHLER.)

Order 20. Umbelliflorae

Inflorescence as a rule an umbel. Flowers hermaphrodite, actinomorphic; a single whorl of stamens and an inferior bilocular ovary, the upper surface of which forms the nectary. Carpels two. A single pendulous ovule in each loculus.

Family 1. **Cornaceae.**—*Cornus mas,* the Cornelian Cherry (Fig. 752), expands its umbels of tetramerous yellow flowers before the leaves appear. Each umbel is subtended by four bracts. The inflorescences for the succeeding year are already present in the axils of the leaves by the time the fruit is ripe. In Britain two species of *Cornus* occur: *C. sanguinea,* the Dogwood, and *C. suecica,* an arctic and alpine plant which reaches its southern limit in Germany.

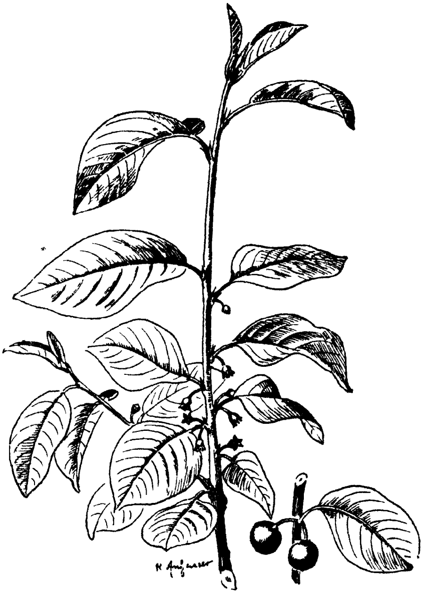


FIG. 748.—*Rhamnus Frangula* (½ nat size). Flowering branch and portion of a branch bearing fruits.

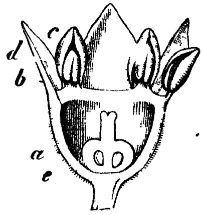


FIG. 749.—*Rhamnus Frangula.* Flower cut through longitudinally. *a*, Receptacle; *b*, calyx; *c*, petal; *d*, a stamen; *e*, pistil (magnified). (After BERG and SCHMIDT.)

Family 2. **Araliaceae.**—In Britain the only representative of the family is the Ivy (*Hedera Helix*) (42), a root-climber. The elliptical pointed leaf-form appears on the orthotropous shoots of older plants, which in late summer or autumn bear the flowers. The leaves of the creeping or climbing plagiotropous shoots are lobed and usually have shorter stalks. Calyx with five pointed sepals corresponding to the five ribs on the inferior ovary. The corolla is greenish in tint, the large disc on the upper surface of the ovary attracts the visits of flies and bees. The fruits ripen during the winter and become blackish blue berries, these are eaten by birds and in this way the seeds are distributed

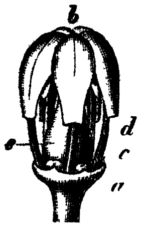


FIG 750 —*Vitis vinifera* Opening flower *a* Calyx *b* corolla *c* disc *d* stamens *e* ovary (Magnified After BERG and SCHMIDT)

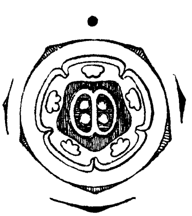


FIG 751 —Floral diagram of *Ampelopsis hederacea* (After EICHLER)

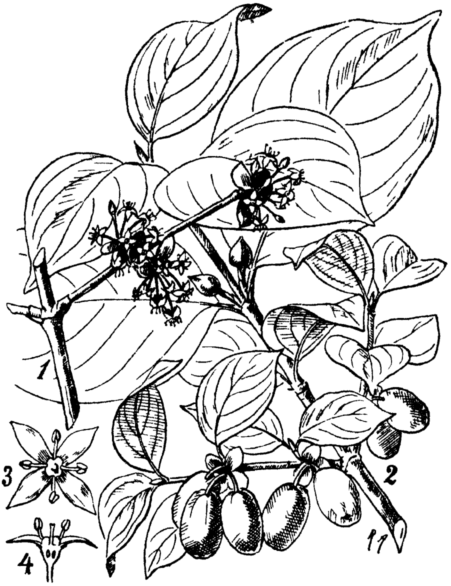


FIG 752 —*Cornus mas* (½ nat size) *1* Flowering twig *2* Twig with fruits *3* Flower seen from above *4* Flower in longitudinal section (*3 4* enlarged)

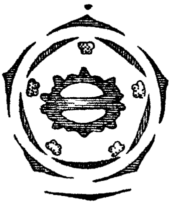


FIG 753 —Umbelliferae Floral diagram (*Siler*) (After NOLL)

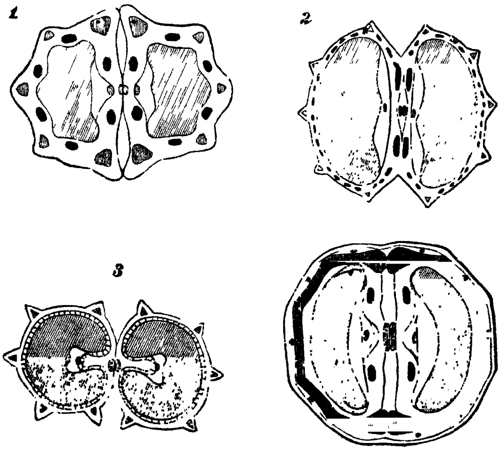


FIG 754 —Fruits of Umbelliferae in cross section *1*, *Foeniculum capillaceum* *2*, *Pimpinella anisum* *3* *Conium maculatum* *4*, *Coriandrum sativum* (*4* modified after a figure by DRUDE)

Family 3. **Umbelliferae** (42a).—Herbaceous plants, sometimes of large size. The stem, which has hollow internodes and enlarged nodes, bears alternate leaves; these completely encircle the stem with their sheathing base, which is often of large size. The leaves are only rarely simple; usually they are highly compound. Inflorescence terminal, frequently overtopped by the next younger lateral shoot. It is an umbel, or more frequently a compound umbel, the bracts forming the involucre and partial involucres, or an involucre may be wanting. Flowers white, greenish, or yellow; other colours are rare. K 5, C 5, A 5, G$(\underline{2})$. The sepals are usually represented by short teeth. The flowers at the circumference of the compound umbel sometimes become zygomorphic by the enlargement of the outwardly directed petals. Ovary always bicarpellary and bilocular; in each loculus a single ovule which hangs from the median septum with its micropyle directed upwards and outwards. The upper surface of the carpels is occupied by a swollen, nectar-secreting disc continuing into the longer or shorter styles, which terminate in spherical stigmas. Fruit, a schizocarp, splitting in the plane of the septum into two partial fruits or mericarps. In many cases the latter remain for a time attached to the carpophore, which originates from the central portion of the septum; this separates from the rest of the septum and bears the mericarps hanging from its upper forked end (Figs 753-758).

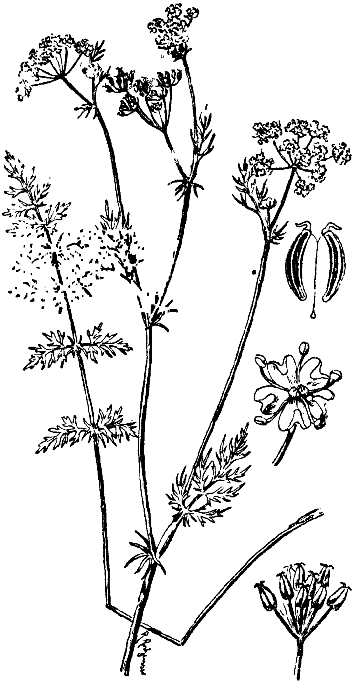


Fig. 755.—*Carum carvi* (½ nat. size). Inflorescence bearing fruits. Single flower, and carpophore bearing the mericarps (enlarged).

The main areas of distribution of the Umbelliferae are the steppe region of Western Asia, Central North America, Chile, and Australia.

For systematic purposes the fruits are of great importance. Each half of the fruit has five ribs, beneath which the vascular bundles lie. The marginal ribs of each partial fruit frequently lie close together at the septum or they may be distinct; they may resemble the three dorsal ribs or differ more or less from them.

Between the five primary ribs four secondary ribs are sometimes present. Usually furrows (valleculae) occur between the ridges, and beneath each furrow a large oil-duct (vitta) is found, extending the whole length of the fruit. On either side of the carpophore a similar oil-duct is present in the septum, so that each mericarp has six of these vittae (Fig. 754, 1). In some species additional small ducts are present (Fig. 754, 2, 3). The form of the fruit as seen in a cross-section differs according to whether the diameter is greater in the plane of the septum or at right angles to this. The character of the marginal and dorsal ridges and the presence or absence of secondary ridges or vittae serve to distinguish the fruits, and are indispensable aids in determining the species. Since many of the fruits are employed in medicine or as spices, while others are poisonous, their

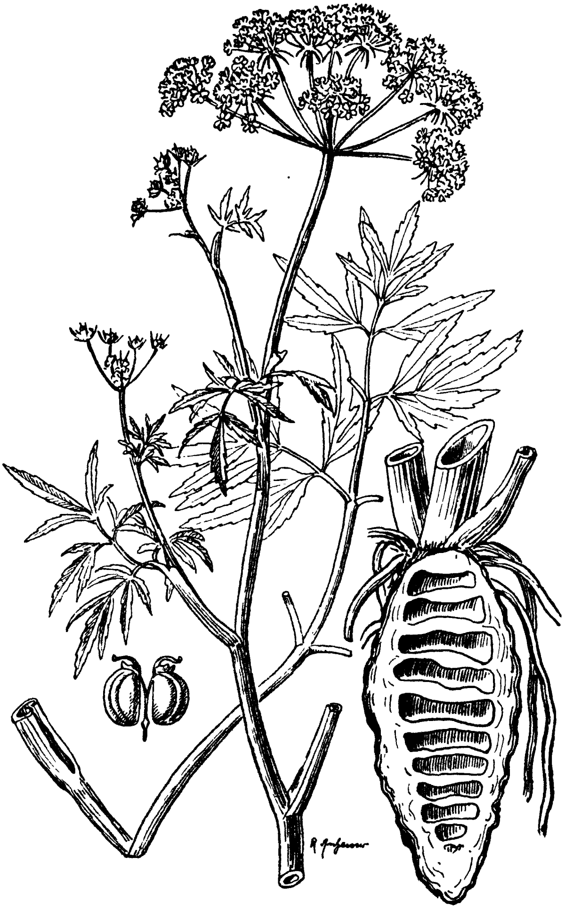


FIG. 756.—*Cicuta virosa.* Rhizome cut through longitudinally (½ nat. size). Fruit (enlarged). *POISONOUS.*

distinction becomes a matter of importance. The endosperm of the seeds contains a fatty oil as reserve-material.

In the following genera the endosperm is flat or slightly convex on the ventral side (Fig. 754, 1, 2). *Pimpinella*, Burnet-Saxifrage. *P. anisum*, Anise, is an annual plant, the seedlings of which exhibit increasing subdivision of the lamina in successive leaves. *Carum carvi*, Carraway, has long been cultivated (Fig. 755); leaves bipinnate, the lowest pinnae resembling stipules. The large lower pinnules are usually placed horizontally on the vertical rachis of the leaf; the terminal pinnules are simple and linear. The terminal umbel, the flowers of which open first, is overtopped by the lateral umbels arising from the leaf-axils. Biennial. *Foeniculum* (Fennel) and *Levisticum* (Lovage) have yellow flowers. *Petroselinum* (Parsley), *Pastinaca* (Parsnip), *Daucus* (Carrot), *Apium* (Celery), and *Anethum* (Dill), are used as vegetables. *Cicuta* (Water-Hemlock, Fig. 756), *Sium* (Water-Parsnip), *Oenanthe* and *Berula*, are marsh- or water-plants. *Aethusa cynapium* (Fool's Parsley, Fig. 757) has the ribs of the fruit keeled; umbels with three elongated, linear, involucral leaves directed outwards. All the last-named plants are poisonous. *Archangelica officinalis*, which is used for food in the far north, is a conspicuous plant, reaching a height of two metres, with large,

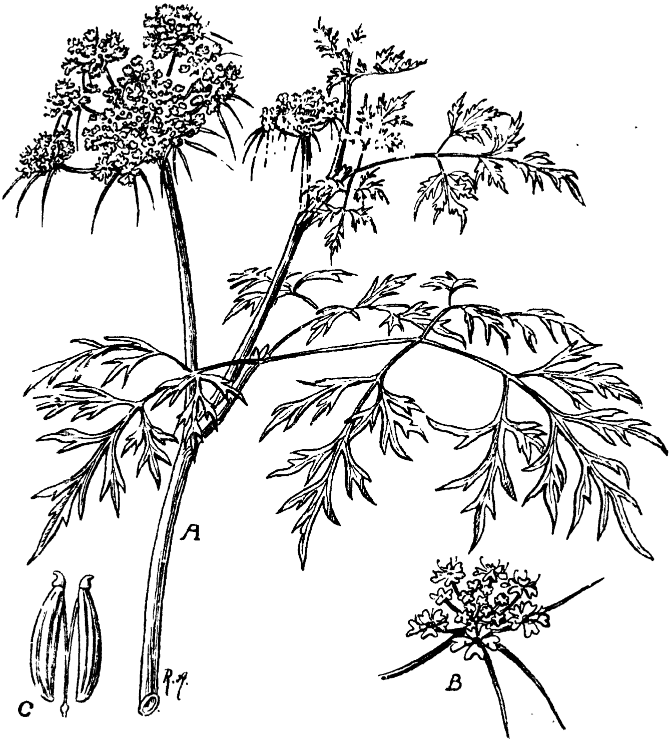


FIG. 757.—*Aethusa cynapium* (⅔ nat. size). *B*, Single umbel. *C*, Fruit (enlarged). *POISONOUS.*

bipinnate leaves provided with saccate sheathing bases; the greenish flowers are markedly protandrous.

In the following genera the ventral side of the endosperm is traversed by longitudinal groove. *Scandix*, *Anthriscus* (Beaked Parsley), *Chaerophyllum* (Chervil). *Conium maculatum*, the Hemlock, is a biennial plant, often of considerable height; it is completely glabrous, the stem and leaf-stalks often with purple spots; leaves dull green, bi- to tri-pinnate. The ultimate segments end in a small, colourless, bristle-like tip. Fruit with wavy, crenate ridges and without oil-ducts in the valleculae. The whole plant has a peculiar, unpleasant odour (Fig. 758).

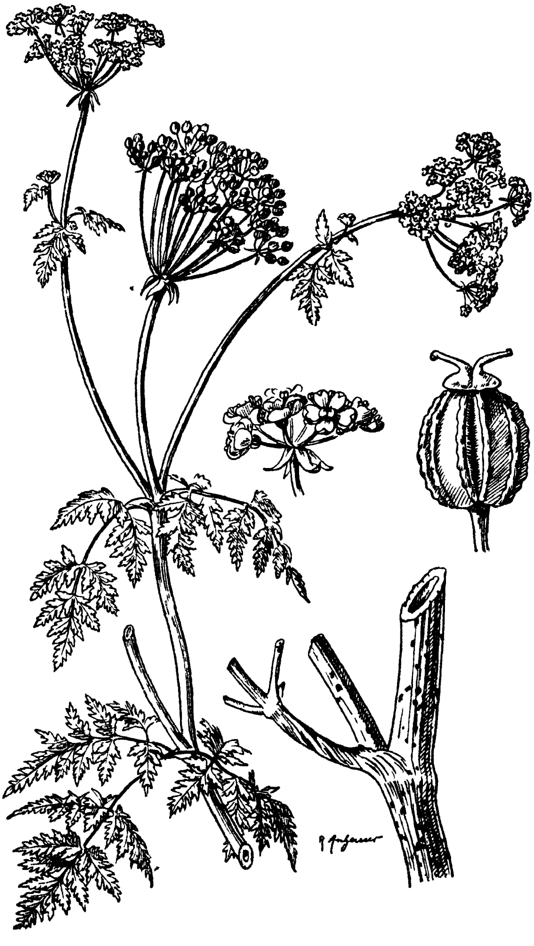


Fig. 758.—*Conium maculatum* (½ nat. size). POISONOUS

The ventral side of the endosperm is concave (Fig. 754, 4). *Coriandrum sativum* is an annual plant; flowers zygomorphic owing to the enlargement of the sepals and petals at the periphery of the umbel. Fruit spherical; mericarps closely united, with ill-marked primary ridges and somewhat more distinct secondary ridges.

• OFFICIAL. — *Ferula foetida* (Persia), ASAFETIDA. *Dorema Ammoniacum* (Persia), AMMONIACUM. *Pimpinella Anisum*, ANISI FRUCTUS. *Coriandrum sativum*, CORIANDRI FRUCTUS. *Foeniculum vulgare*, FOENICULI FRUCTUS. *Carum carvi*, CARUI FRUCTUS. *Carum copticum*, THYMOL, OLEUM AJOWAN. *Anethum* (*Peucedanum*) *graveolens*, ANETHI FRUCTUS.

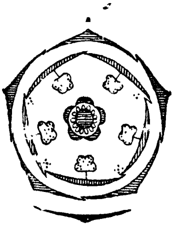


FIG. 759.—Primulaceae. Floral diagram (*Primula*).

B. Sympetalae

The only character common to the Sympetalae is the gamopetalous corolla. The first three orders, the Primulales, Bicornes, and Diospyrales have as a rule five whorls of members in their flowers and are classed as Pentacyclicae. All the other Sympetalae have only one staminal whorl and are therefore termed Tetracyclicae. The Sympetalae have as a rule ovules with only one integument. It is clear that the Sympetalae do not constitute a natural group and frequent attempts have been made to distribute them in relation to the various series of the Choripetalae. In the survey given at the beginning of the system the connections of various orders of Sympetalae to the Choripetalae is indicated so far as these seem probable on morphological and serological grounds. Since the Primulales and the Bicornes both possess some choripetalous genera and species, these orders stand nearest to the Choripetalae. The Primulales connect with the Centrospermae by reason of the free-central placentation. The poricidal anthers that characterise the Bicornes are met with in some, but not all, Guttiferae, so that a connection with this group of Choripetalae seems possible.

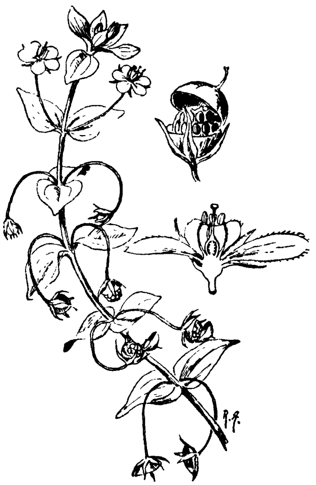


FIG. 760.—*Anagallis arvensis* (½ nat. size). Longitudinal section of flower, and capsule at dehiscence (enlarged).

A. PENTACYCLICAE

Order 21. Primulales

Family 1. **Primulaceae.**—The floral diagram (Fig. 759) shows only one whorl of stamens; these stand opposite the petals, the outer whorl of stamens being absent.

The free-central placentation is characteristic. The genus *Primula* is widely distributed; the British species show the superior unilocular ovary with a single style, characteristic of the family; dimorphic heterostyly (Fig. 567). *Anagallis* (Fig. 760), capsule opens by a lid. *Cyclamen* (Fig. 761). The uncooked tubers of *Cyclamen*, the plant of *Anagallis*, and the glandular hairs of a number of species of *Primula* (*P. obconica*, *Corthusa matthioli*[43]) are poisonous.

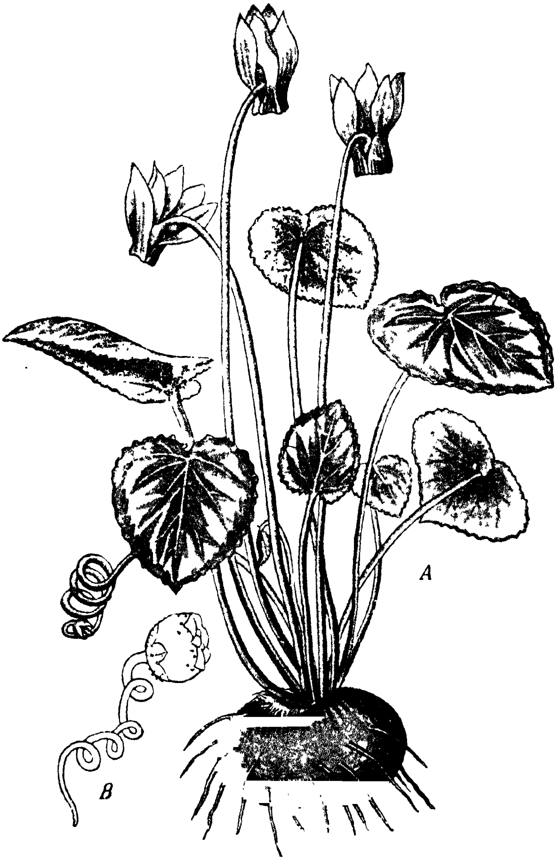


FIG 761.—*Cyclamen europaeum* *A* Entire plant (reduced). *B*, Fruit with spirally coiled stalk that carries it into the soil. (After REICHENBACH.) *POISONOUS*

Order 22. Bicornes

Family 1. **Ericaceae** ([44]) —Evergreen, shrubby plants with small, often needle-shaped leaves. Anthers characterised by the possession of an "exothecium" (p. 554), opening by pores or splits, frequently provided with horn-like appendages, on which account the group is also termed Bicornes.

Flowers which are pentamerous in all five whorls are found in the species of

Rhododendron or Alpine Rose, in *Ledum palustre*, and *Andromeda*, all these have a capsular fruit derived from the superior ovary *Arctostaphylos Uva ursi* is similar, but the fruit is a drupe (Fig 762) Pentamerous flowers with an inferior ovary which becomes a berry are found in the genus *Vaccinium* (Fig 763), *V. vitis idea*, Cowberry, *V myrtillus*, Blaeberry. The remains of the calyx persist on the summit of the fruit A reduction of the number of members of the whorls to four is met with in the genus *Erica* with a superior ovary many species being native to the Mediterranean region and the Cape *Erica tetralix* is distinguished from the closely related Heather, *Calluna vulgaris*, by its corolla being longer than the calyx, both are abundant in Britain

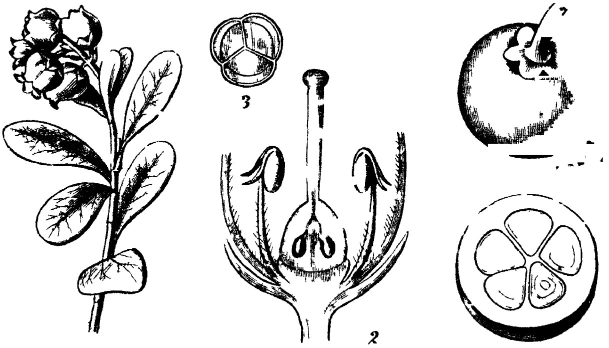


FIG 762.—*Arctostaphylos Uva ursi* 1 Flowering branch 2 Flower in longitudinal section 3 Pollen tetrad 4, Fruit 5 Fruit in transverse section (2-5 enlarged After BERG and SCHMIDT)

OFFICIAL — *Arctostaphylos Uva ursi* yields UVAE URSI FOLIA

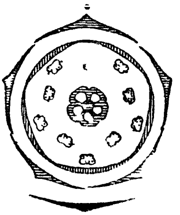


FIG 763 —Floral diagram of *Vaccinium* (Ericaceae) (After NOLL)

Order 23 Diospyrales

The **Sapotaceae** is a tropical family the plants contain latex Species of *Palaquium* (Fig 764) and *Payena* from the Malayan Archipelago are the trees from which gutta percha is obtained Balata is obtained from *Mimusops*, trees found throughout the tropics

Ebenaceae —*Diospyros Kaki* is a Japanese fruit tree, *D Ebenum*, ebony

Styracaceae —OFFICIAL—BENZOINUM from *Styrax Benzoin*

B. Tetracyclicae

Plants, the flowers of which have four whorls of members. Those with a superior ovary may be placed first. There are always two carpels present, the flowers may be actinomorphic or zygomorphic The actinomorphic forms may be treated first

1 *Ovary Superior*

Order 24. Contortae

Plants with decussate, usually simple leaves and actinomorphic flowers, the corolla of which is often contorted in the bud. Stamens epipetalous. Carpels two, superior. Frequently with bi-collateral vascular bundles, or strands of sieve-tubes in the wood.

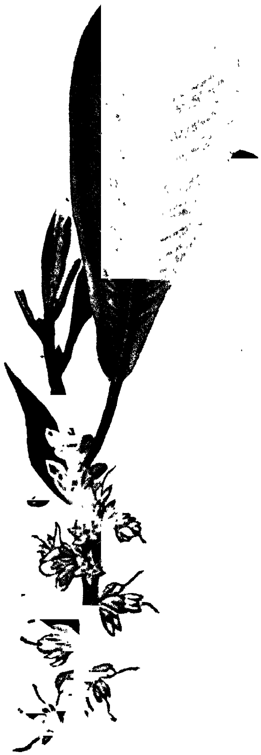


Fig. 764.—*Palaquium Gutta.* (½ nat. size. After A. Meyer and Schumann.)

According to serological discoveries the families are related. Derivation from the Choripetalae leads to forms with two superior carpels (*Mercurialis*, Polygalaceae, Aceraceae, etc., Gruinales); those with contorted aestivation (Malvaceae) and those with the androecium adherent to the corolla (Columniferae). Thus the orders Columniferae and Gruinales may be regarded as related to the Contortae.

Family 1. **Oleaceae.**—This is readily recognised by the two stamens. The corolla is usually tetramerous as is shown in the floral diagram of *Syringa* (Fig. 765). Besides *Ligustrum*, *Jasminum* and *Syringa*, *Olea europaea*, the Olive Tree or Olive, is the most important plant of the family (Fig 766). It is a native of the Mediterranean region, where it is also cultivated. The flower and fruit correspond to the type for the family (Fig. 766, 767). The drupe contains a fatty oil both in the succulent exocarp and in the endosperm (Fig 768). *Fraxinus*, the Ash, differs from the type of the order in having pinnate leaves; *F. excelsior* has apetalous, anemophilous flowers, which appear before the leaves. *F. ornus*, the Flowering Ash, has a double perianth and is entomophilous; it is polygamous, having hermaphrodite flowers as well as female flowers with black sterile anthers; the corolla is divided to the base. It is cultivated in Sicily for the sake of the mannite it yields.

OFFICIAL. — *Olea europaea* yields OLEUM OLIVAE

Family 2 **Loganiaceae** ([45]).—Species of *Strychnos*, yield the well-known CURARE of South America, and the arrow poison used by the Malays. *Spigelia* has ruminated endosperm.

OFFICIAL. —*Strychnos nux vomica* (Fig. 770), yields NUX VOMICA and STRYCHNINA. GELSEMII RADIX is obtained from *Gelsemium nitidum*, which is a native of North America.

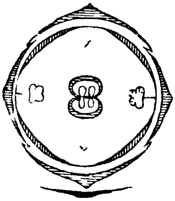


FIG. 765.—Oleaceae. Floral diagram (*Syringa*).

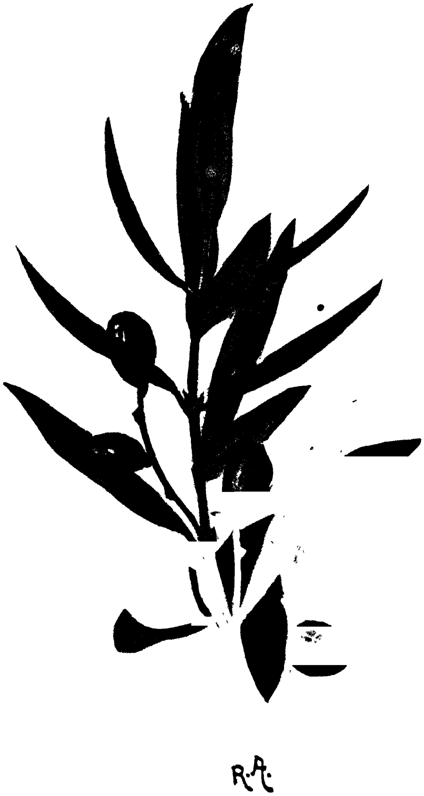


FIG. 766.—*Olea europaea* in fruit (½ nat. size).

Family 3. **Gentianaceae.**—This is recognisable by the unilocular ovary and the clearly contorted corolla when in bud (Fig. 771). *Gentiana* ([46]) is a genus with numerous species, the large, brightly coloured, usually blue flowers of which are a feature of the flora of the Alps. *Erythraea*, Centaury. *Menyanthes*, Bog-Bean. *Limnanthemum*, aquatic plants with floating leaves.

OFFICIAL.—*Gentiana lutea* and other species yield GENTIANAE RADIX. CHIRATA is obtained from *Swertia chirata* (North India).

Family 4. **Apocynaceae.**—Evergreen plants with latex. Especially numerous in the tropics. Stigma ring-shaped. Carpels only united in the region of the style, free below and separating after fertilisation. Usually two follicles with numerous seeds provided with a tuft of hairs (Fig. 774).

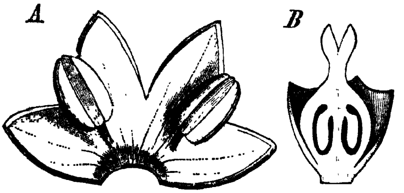


FIG. 767.—*Olea europaea.* *A*, Corolla spread out. *B*, Calyx and ovary in longitudinal section. (Enlarged. After ENGLER-PRANTL.)

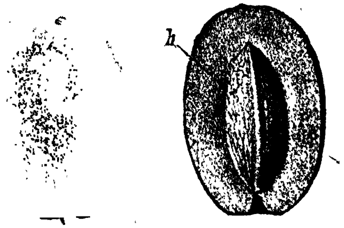


FIG. 768.—*Olea europaea.* Drupe. *h*, Stone.

The only British species is *Vinca minor*, the ever-green Periwinkle, occurring in woods (Fig. 772). *Nerium oleander* (Fig. 773), a native of the Mediterranean region. The floating fruit of *Cerbera Odollam*, from the mangrove vegetation, is shown in Fig. 613.

OFFICIAL.—*Strophanthus kombe* (47) (Fig. 774), lianes of tropical Africa, yield STROPHANTHI SEMINA. ALSTONIA is obtained from *Alstonia scholaris*.

Caoutchouc (32, 48), is obtained from *Kickxia elastica* and other species, trees of tropical West Africa. It is also obtained from numerous species of *Landolphia* (*L. Kirkii*, *Heudelotii*, *comorensis*, etc.), and species of *Carpodinus* from tropical Africa. *Hancornia speciosa*, a tree of the dry Brazilian Campos, and *Willoughbeia firma*, *W. flavescens*, and other species of this Malayan genus of lianes, are also rubber-yielding plants. Gutta-percha is present in the latex of *Tabernaemontana Donnell Smithii*, Central America.

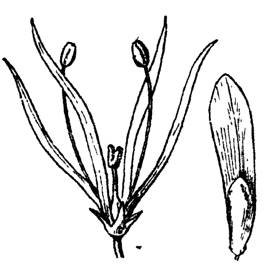


FIG. 769.—*Fraxinus ornus.* Flower and fruit.

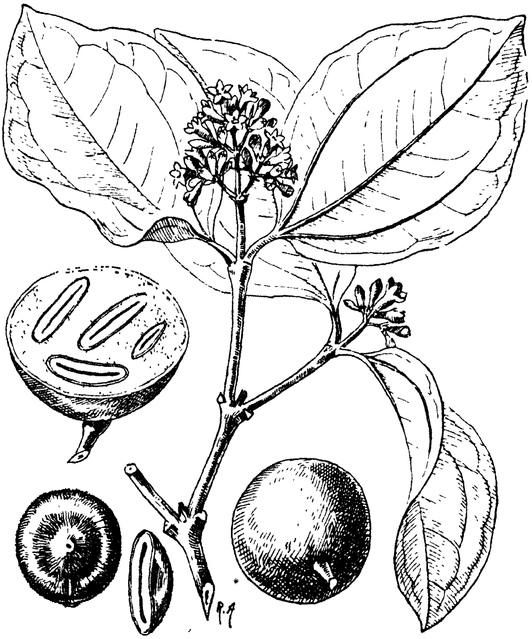


FIG. 770.—*Strychnos nux vomica* (½ nat. size). Fruit and seed whole and in cross-section. *POISONOUS.*

Family 5. **Asclepiadaceae.**—Similar and closely related to the Apocynaceae but differing in the carpels being free, only united by the prismatic stigma (Fig. 775). Stamens united at the base, with dorsal, nectar-secreting appendages forming a corona. The pollen of each pollen-sac is united into a pollinium, the stalk of which is attached to a glandular swelling (adhesive disc) of the angular stigma. These adhesive discs alternate with the stamens so that the two pollinia attached to each disc belong to the halves of two adjoining stamens. Visiting insects remove the pollinia, as in the Orchidaceae, and carry them to another flower (Fig. 775).

Vincetoxicum officinale (Fig. 776) is a European herb with inconspicuous white flowers and hairy seeds which are borne in follicles; poisonous. Other Asclepiadaceae are mostly tropical or sub-tropical. The succulent species of *Stapelia*, *Hoodia*, *Trichocaulon*, etc. (pp. 165-66, Fig. 194 *a*), which resemble Cactaceae in habit, and inhabit South African deserts, and *Dischidia rafflesiana* (49), the peculiar pitcher-plant of the Malayan region (p. 175, Fig. 206), the pitchers of which serve to condense water, deserve special mention. *Hoya carnosa* and many species of *Ceropegia* are frequently cultivated.

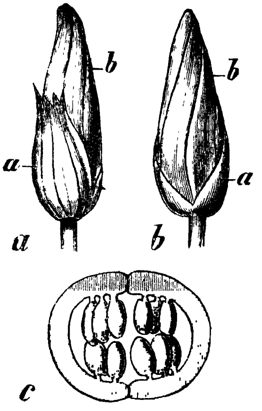


FIG. 771.—*Gentiana lutea*. *a* and *b*, Flower-buds (nat. size), showing calyx (*a*) and twisted corolla (*b*); *c*, transverse section of ovary. (After BERG and SCHMIDT.)

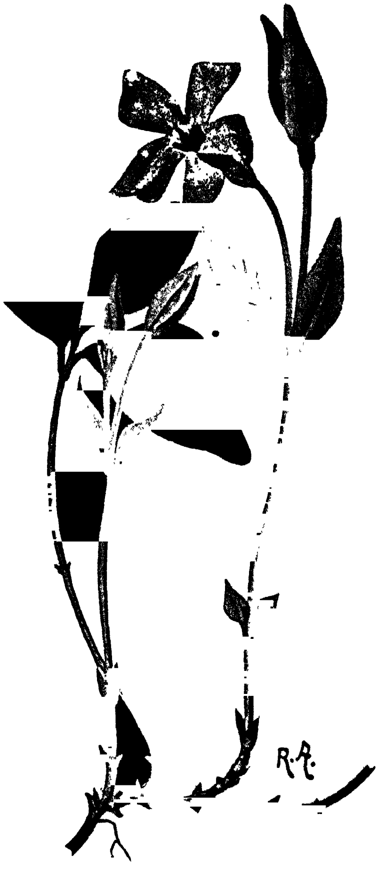


FIG. 772.—*Vinca minor* (⅔ nat. size).

Corresponding to the actinomorphic Contortae as further derived forms are the Tubiflorae and Personatae which are mostly zygomorphic; these also can thus be traced back to the Columniferae and Gruinales.

Order 25. Tubiflorae

Flowers pentamerous, actinomorphic, or zygomorphic. Carpels two. Ovary superior, bilocular, with two ovules, which are frequently separated by a false septum, in each loculus. The normal number of stamens is reduced in the zygomorphic flowers to four or two.

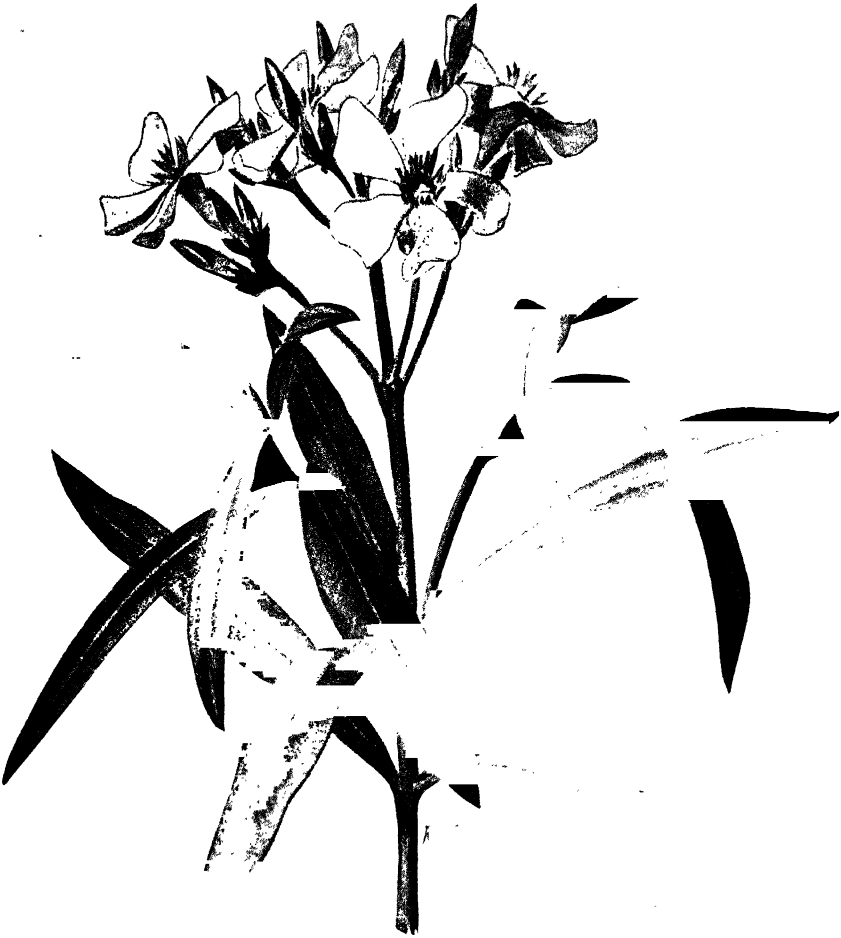


FIG. 773.—*Nerium oleander* (½ nat. size). POISONOUS.

Family 1. **Convolvulaceae.**—Many of the plants of this family are twining plants with alternate sagittate leaves, and wide, actinomorphic, funnel-shaped corolla, which is longitudinally folded in the bud. Ovules erect; fruit, a capsule.

Convolvulus arvensis, a perennial, twining, herbaceous plant occurring everywhere by waysides, and as a weed in cornfields Flowers solitary, long stalked, situated in the axils of the leaves and sometimes in the axils of the bracteoles of

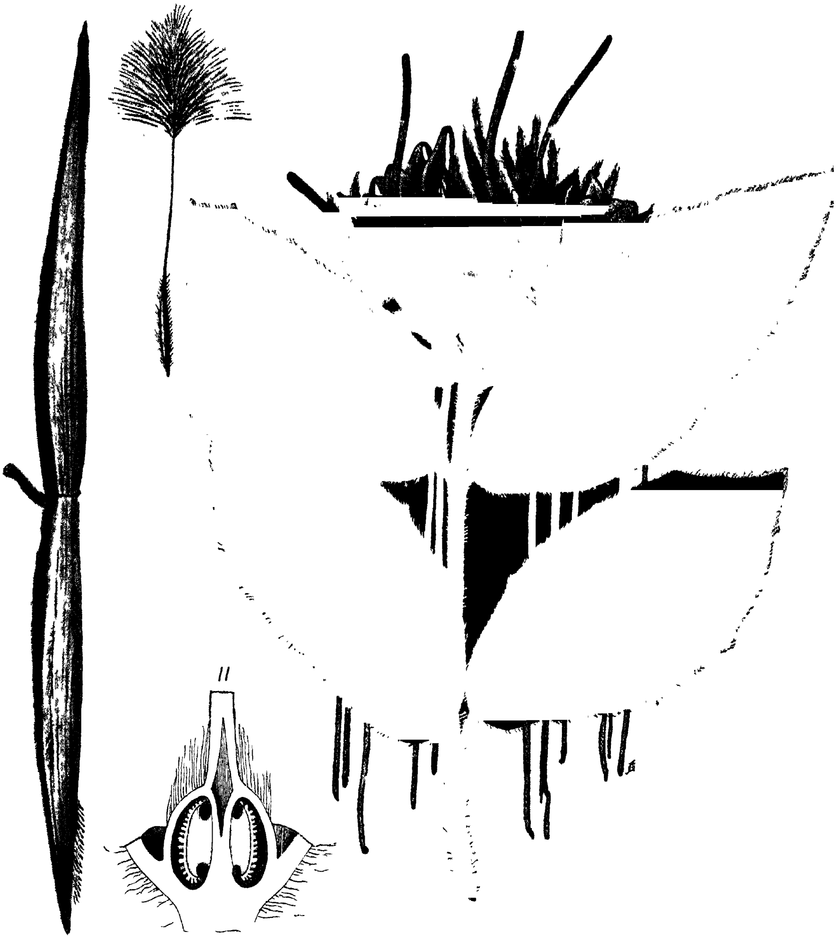


FIG 774 —*Strophanthus hispidus* (½ nat size After F Gilg and Meyer and Schumann) Ovary in longitudinal section ($\frac{10}{1}$) Fruit (1 nat size) Seed (½ nat size) (After Schumann in Engler Prantl)

another flower *Calystegia* has two large bracteoles placed immediately beneath the calyx *C sepium.* The Dodder (*Cuscuta*) is a slender parasitic plant, with slender stems and clusters of small flowers, which attaches itself by means of haustoria to a number of different host plants (Fig 214). *Ipomoea* several species are cultivated as ornamental plants *I pescaprae* is one of the strand-plants of tropical countries *Pharbitis* is closely related (p 346, Fig. 282)

OFFICIAL.—JALAPA is obtained from *Ipomoea* (*Exogonium*) *purga* (Fig. 777), a twining plant, with tuberous lateral roots, occurring on the wooded eastern slopes of the Mexican tableland. *Ipomoea hederacea* yields KALADANA, *I. orizabensis* yields IPOMOEA RADIX, *I. turpethum* yields TURPETH. SCAMMONIAE RADIX is the dried root of *Convolvulus Scammonia* (Asia Minor).

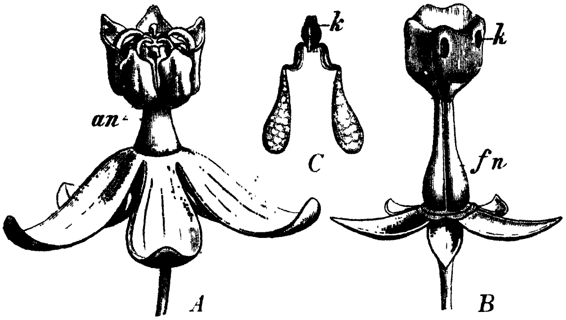


FIG. 775.—*Asclepias curassavica.* *A*, Flower; *an*, androeceum (× 4). *B*, Calyx and gynaeceum; *fn*, ovary; *k*, adhesive discs (× 6) *C*, Pollinia (more highly magnified) (After BAILLON.)

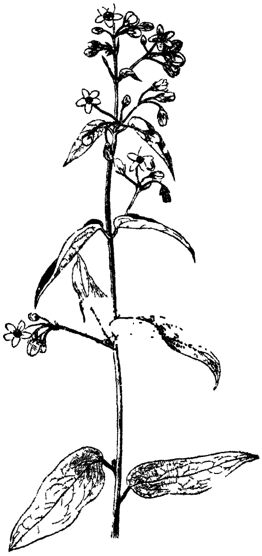


FIG. 776.—*Vincetoxicum officinale* (⅓ nat. size). POISONOUS.

FIG. 777.—*Ipomoea* (*Exogonium*) *purga* (½ nat. size. After BERG and SCHMIDT).

Family 2. **Boraginaceae.**—Contains herbs usually covered with coarse hairs. *Symphytum* (Comfrey), *Borago* (Borage), *Anchusa* (Alkanet), *Myosotis* (Forget-me-not) with actinomorphic flowers, and *Echium*, in which the flowers are slightly zygomorphic, are among the commonest and most conspicuous herbaceous plants of our flora; inflorescence a cincinnus or double cincinnus. Petals frequently provided with scales standing in the throat of the corolla. Ovary always bilocular but divided by false septa into four one-seeded nutlets. The style springs from the midst of the four-lobed ovary (Fig. 778).

Family 3. **Verbenaceae.**—Clearly dorsiventral flowers, with only four stamens; the ovary contains only four ovules (Fig. 779 *A*), but the style is terminal. *Tectona grandis*, Teak-tree; *Avicennia* (49) a viviparous mangrove plant.

Family 4. **Labiatae.**—Distributed over the earth. Herbs or shrubs with quadrangular stems and decussate leaves without stipules. Leaves simple; plants often aromatic owing to the presence of glandular hairs. The small inflorescences are dichasia or double cincinni. Flower zygomorphic (Fig. 779 *B*). Calyx gamosepalous, with five teeth; corolla two-lipped, the upper lip consisting of two, the lower of three petals; stamens in two pairs, two long and two short, rarely only two (*Salvia*, *Rosmarinus*). The ovary (Fig. 779 *B*) corresponds to that of the Boraginaceae and Verbenaceae; it has a ring-shaped nectary at the base.

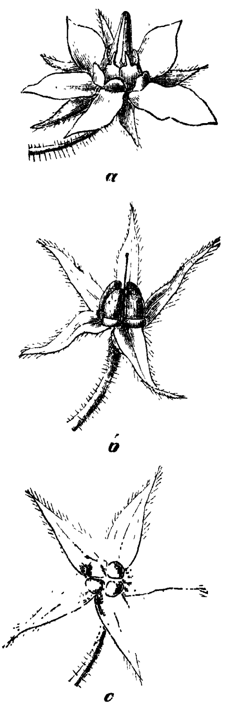


FIG. 778.—*Borago officinalis*. *a*, Flower; *b* and *c*, fruit (nat. size).

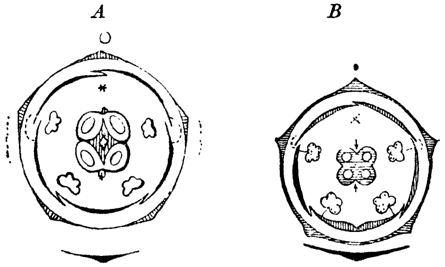


FIG. 779.—Floral diagrams of (*A*) *Verbena officinalis* (after EICHLER), and (*B*) *Lamium* (Labiatae) (after NOLL).

The Labiatae include a considerable proportion of our commonest native spring and summer flowers; *Lamium*, *Galeopsis* (Fig. 780), and *Stachys* have the upper lip helmet-shaped, *Ajuga* has it very short, while in *Teucrium* the upper lip is deeply divided. *Nepeta* and *Glechoma* differ from the majority of the order, in having the posterior stamens longer than those of the anterior pair. *Salvia*, Sage, has the two stamens that remain peculiarly constructed in relation to pollination (cf. p. 567, Fig. 562, Fig. 782). Many Labiatae are of value on account of their aromatic properties. They are especially abundant in the xerophytic formation of shrubby plants in the Mediterranean region to which the name Maquis is given.

OFFICIAL.—*Rosmarinus officinalis* yields OLEUM ROSMARINI. *Lavandula vera*

(Fig. 781) (Mediterranean region), OLEUM LAVANDULAE. *Mentha piperita*, OLEUM MENTHAE PIPERITAE. *M. viridis*, OLEUM MENTHAE VIRIDIS. *M. arvensis* and vars. *piperascens* and *glabrata* yield MENTHOL. *Thymus vulgaris* and *Monarda punctata* yield THYMOL.

Order 26. Personatae

The Personatae also include forms with actinomorphic and zygomorphic flowers. There are, however, no false septa in the ovary, and the number of ovules is usually a larger one.

Family 1. **Solanaceae.**—Herbs or small woody plants, with nearly always actinomorphic flowers. Petals plaited. Ovary bilocular, septum inclined obliquely to the median plane (Fig. 783). Fruit, a capsule or a berry. Seeds with

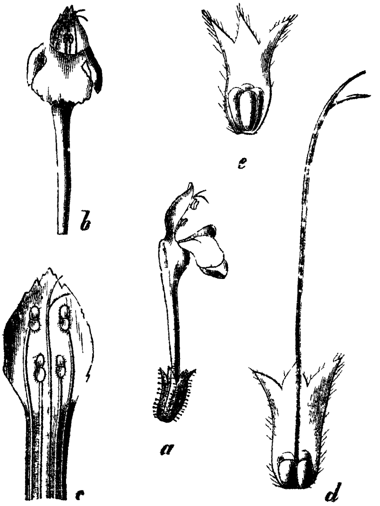


FIG. 780.—*Galeopsis ochroleuca.* *a*, Flower, *b*, the same with calyx removed; *c*, corolla cut open, showing stamens and style; *d*, calyx and gynaeceum; *e*, fruit. (*a*, *b*, nat. size, *c*, *d*, *e*, × 2)

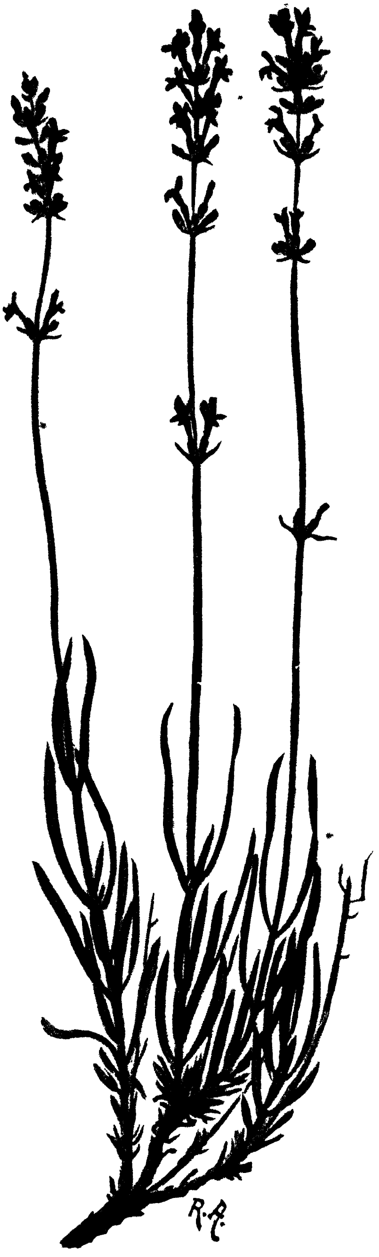


FIG. 781.—*Lavandula vera* (½ nat. size).

endosperm; embryo usually curved. Anatomically the order is characterised by possessing bicollateral vascular bundles.

Many species of *Solanum* occur as weeds. Flowers actinomorphic; fruit, a berry. *S. nigrum*, Night-shade. *S. dulcamara*, Bitter-sweet (Fig. 784). *S. tuberosum*, the Potato. *S. Lycopersicum* (50), the Tomato. On graft-hybrids, periclinal chimaeras and gigas-forms of *Solanum*, cf. p. 301. The Deadly Night-shade, *Atropa belladonna* (Fig. 785), a very poisonous shrubby plant occurring in Europe, is recognisable by the actinomorphic flowers, with a short, wide, tubular corolla of a dirty purple colour and the shining black berries. The main shoot is, to begin with, radial, but branches below the terminal flower into, as a rule, three equally vigorous lateral shoots, which exhibit further cincinnal branching. By the carrying up of the subtending bract upon the lateral shoot an appearance of paired leaves is, brought about. *Capsicum annuum*, Spanish Pepper, has a dry, berry-like fruit. It resembles *Atropa* in its branching and the position of its leaves. *Datura Stramonium*, Thorn-apple (Fig. 786), is an annual plant, widely spread in Europe, Asia, and North America. It has incised, palmately-veined leaves, large, white, terminal flowers, and spiny fruits. *Nicotiana tabacum* (Fig. 787) is a South American plant with numerous cultivated varieties (50a). Its large alternate leaves, which bear numerous glandular hairs, form TOBACCO, after being dried and fermented. *Hyoscyamus niger*, the Henbane (Fig. 788), is an annual poisonous plant of the old world. The alternate, sessile leaves are clothed with glandular hairs. Flowers slightly zygomorphic, of dull yellowish-violet colour with darker markings; inflorescence, a cincinnus. Fruit, a pyxidium.

All Solanaceae are more or less poisonous, partly on account of the presence of considerable amounts of alkaloids which are used in medicine. Species of *Solanum*,

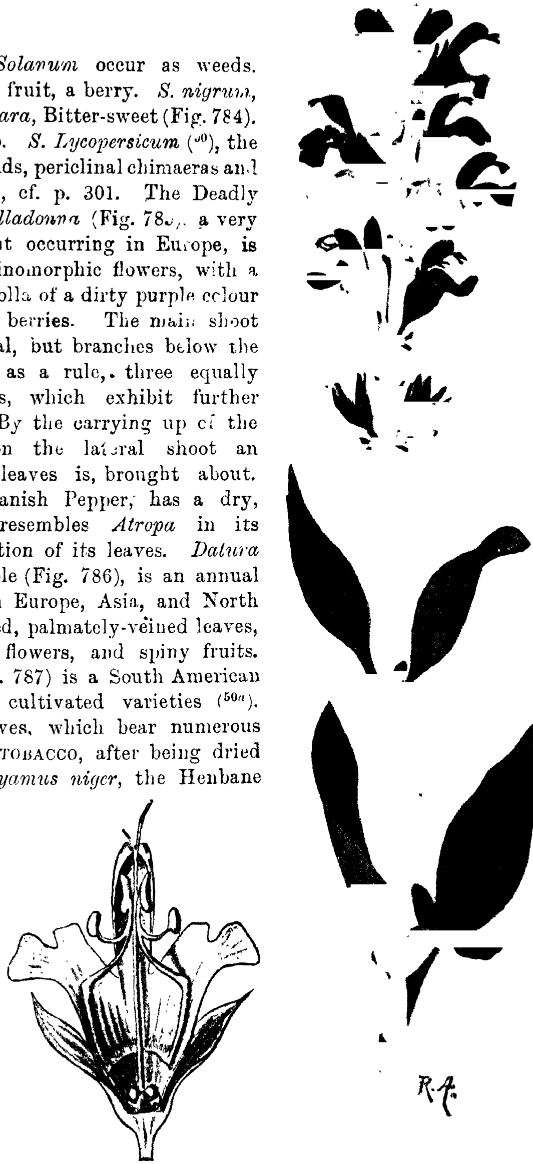


FIG. 782.—*Salvia officinalis*. Flowering shoot (½ nat. size). Tubular corolla slit open to display the stamens (enlarged).

Atropa, *Datura*, *Hyoscyamus*, and *Nicotiana* are among the most poisonous plants met with in this country.

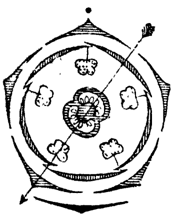


FIG. 783.—Solanaceae. Floral diagram (*Petunia*). (After NOLL.)

OFFICIAL. — *Capsicum minimum* yields CAPSICI FRUCTUS. *Atropa Belladonna* yields BELLADONNAE FOLIA, BELLADONNAE RADIX, and ATROPINA. *Datura Stramonium* yields STRAMONII FOLIA. *D. fastuosa*, var. *alba*, yields DATURA FOLIA and DATURA SEMINA. *D. Metel* yields DATURA FOLIA. *Hyoscyamus niger*, HYOSCYAMI FOLIA.

Family 2. **Scrophulariaceae.** — Flowers zygomorphic. Corolla not plaited in the bud. Number of stamens nearly always incomplete. Carpels median. Fruit, a bilocular capsule.

Verbascum (Fig. 789, 790 *A*), the Mullein; biennial herbs, which in the first season form a large rosette of woolly leaves from which the erect inflorescence arises in the second year. The single flowers have five stamens, and are only slightly zygomorphic; the three posterior stamens have hairy filaments, and are further distinguished from the two anterior stamens by the transverse position of their anthers. *Scrophularia*, *Linaria*, and *Antirrhinum* have a two-lipped corolla with

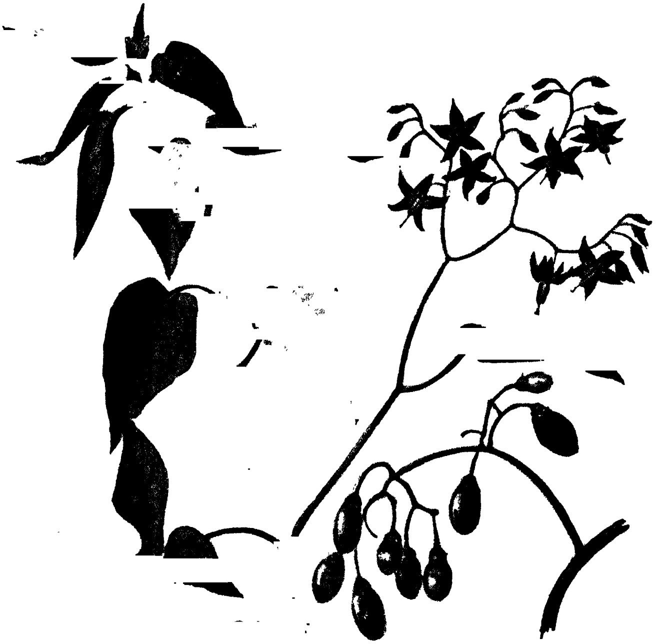


FIG. 784.—*Solanum dulcamara* (½ nat. size). POISONOUS.

four stamens. *Mimulus* and *Torenia*, with irritable stigma (cf. p. 366). *Maurandia* climbs by means of its petioles. *Digitalis*, Foxglove (Fig. 791), has an obliquely campanulate corolla and four stamens. The flowers hang from one side of the ascending raceme, which is produced in the second year. *Gratiola* (Fig. 790 *B*) and *Veronica* with only two fertile stamens.

Fig. 785.—*Atropa Belladonna* (⅓ nat. size). *Poisonous.*

A special group includes a number of closely related genera which have adopted a more or less completely parasitic mode of life. The most completely parasitic form is *Lathraea* (51), the species of which have no trace of chlorophyll; *L. squamaria*, the Toothwort, is parasitic on the roots of the Hazel. Many (*e.g.* *Tozzia*, *Bartsia*, *Euphrasia*, *Odontites*, *Pedicularis*, *Melampyrum*, *Alectorolophus*) are semiparasitic. Although they possess green leaves they attach themselves by means of haustoria to the roots of other plants. On the specially developed haustoria in the ovules of some of these plants cf. Fig. 597.

OFFICIAL.—*Digitalis purpurea* yields DIGITALIS FOLIA. *Picrorhiza kurroa* yields PICRORHIZA.

Family 3. **Orobanchaceae.**—Root-parasites, without chlorophyll. Flower as in the Scrophulariaceae, but with a unilocular ovary. Several British species of *Orobanche*, parasitic on various host-plants (Fig. 792).

Family 4. **Lentibulariaceae.**—Marsh- or water-plants. They capture and digest insects. *Utricularia* (52), *Pinguicula*. Tropical species of *Utricularia* occur as epiphytes.

Family 5. **Plantaginaceae.**—Reduced forms. *Litorella lacustris*. *Plantago*, Plantain (Fig. 566); anemophilous and protogynous.

OFFICIAL.—*Plantago ovata* yields ISPAGHULA.

2. *Ovary Inferior*

Order 27. Rubiales

This order is related to the Umbelliflorae, where also the ovary is inferior. The flowers are tetramerous or pentamerous; the numbers of stamens and carpels vary in the zygomorphic (Caprifoliaceae) and asymmetric (Valerianaceae) flowers.

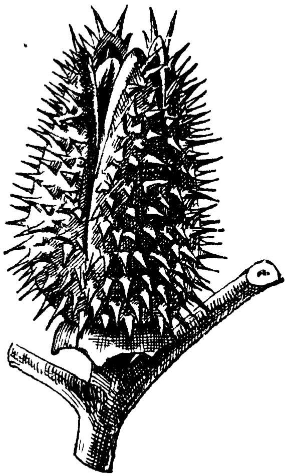


FIG. 786.—*Datura Stramonium* Ripe fruit opening (½ nat. size). *Poisonous.*

The connection of the families of the Rubiales has been proved by serodiagnostic investigations.

The connection between the Umbelliferae and the Rubiaceae is supported by the occurrence in both of tetracyclic flowers, of a bicarpellary, inferior ovary, and of ovules with only one integument. To these characters may be added the expansion of the leaf-base appearing as stipules in the Rubiaceae and as a leaf-sheath in the Umbelliflorae.

Family 1. **Rubiaceae** (53).—Herbs, shrubs, or trees, with simple decussate leaves and stipules. Flowers actinomorphic. Ovary bilocular.

The few native Rubiaceae all belong to the group represented by *Asperula* (Woodruff), *Galium* and *Rubia*. These genera are characterised by the resemblance of the stipules to the leaves; usually a whorl of six members is borne at each node, but sometimes it is reduced to four by the union of the stipules in pairs; the numbers may, however, vary.

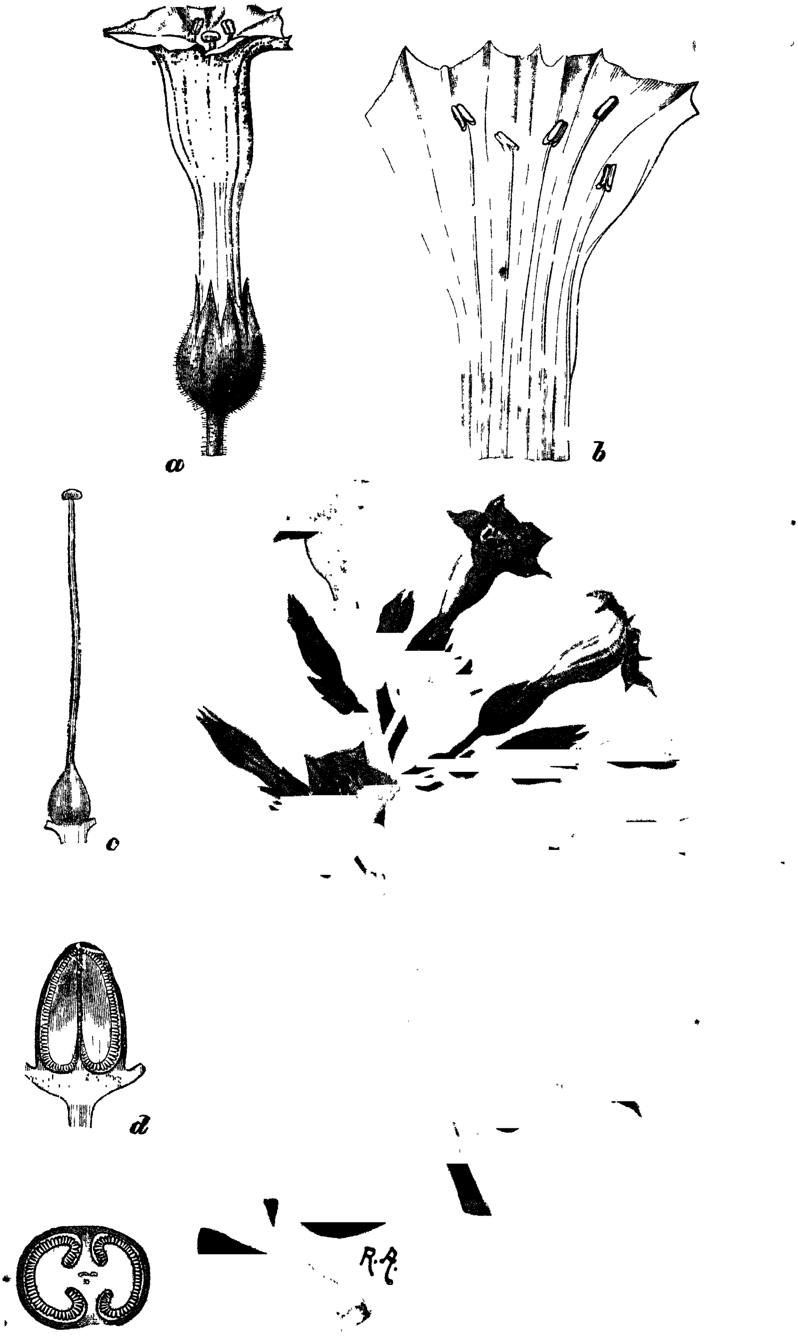


FIG. 787.—*Nicotiana tabacum* (½ nat. size). *Poisonous.* *a*, Flower; *b*, corolla cut open and spread out flat; *c*, ovary; *d* and *e*, young fruit (*a*, *b*, *c*, nat. size; *d*, *e*, × 2.)

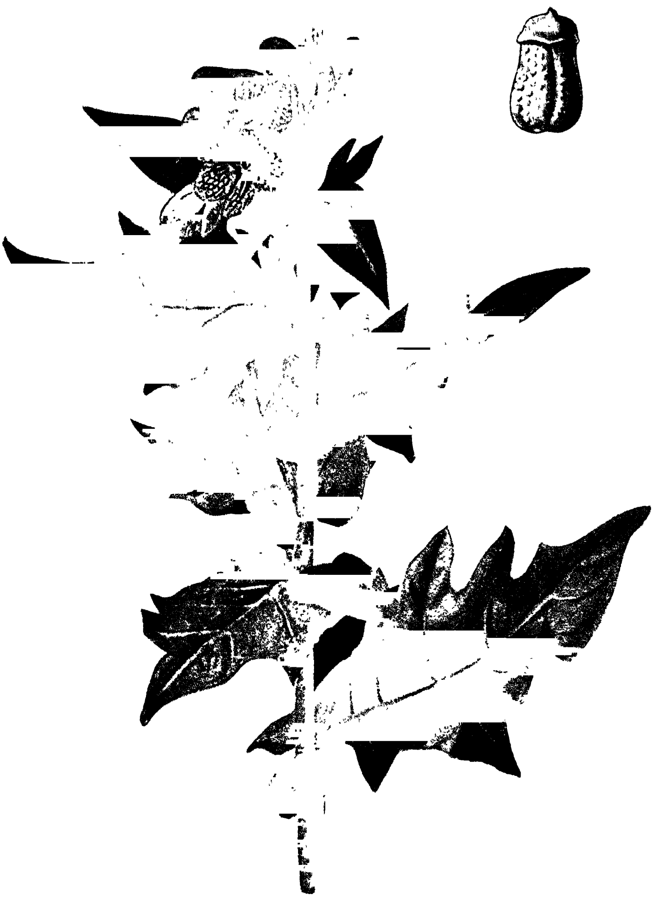


FIG. 788.—*Hyoscyamus niger*. Flowering shoot and fruit (½ nat. size). *Poisonous.*

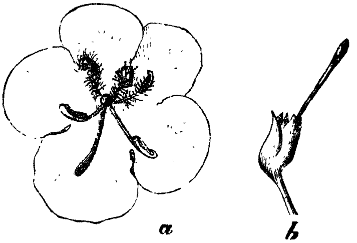


FIG. 789.—*Verbascum thapsiforme*. *a*, Flower; *b*, calyx and style (nat. size). (After H. SCHENCK.)

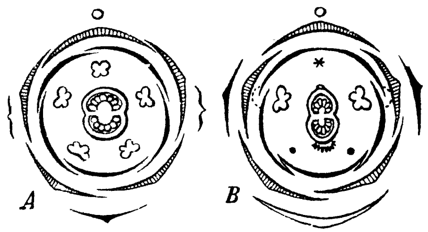


FIG. 790.—Scrophulariaceae. Floral diagrams. *A*, *Verbascum*. *B*, *Gratiola*. (After EICHLER.)

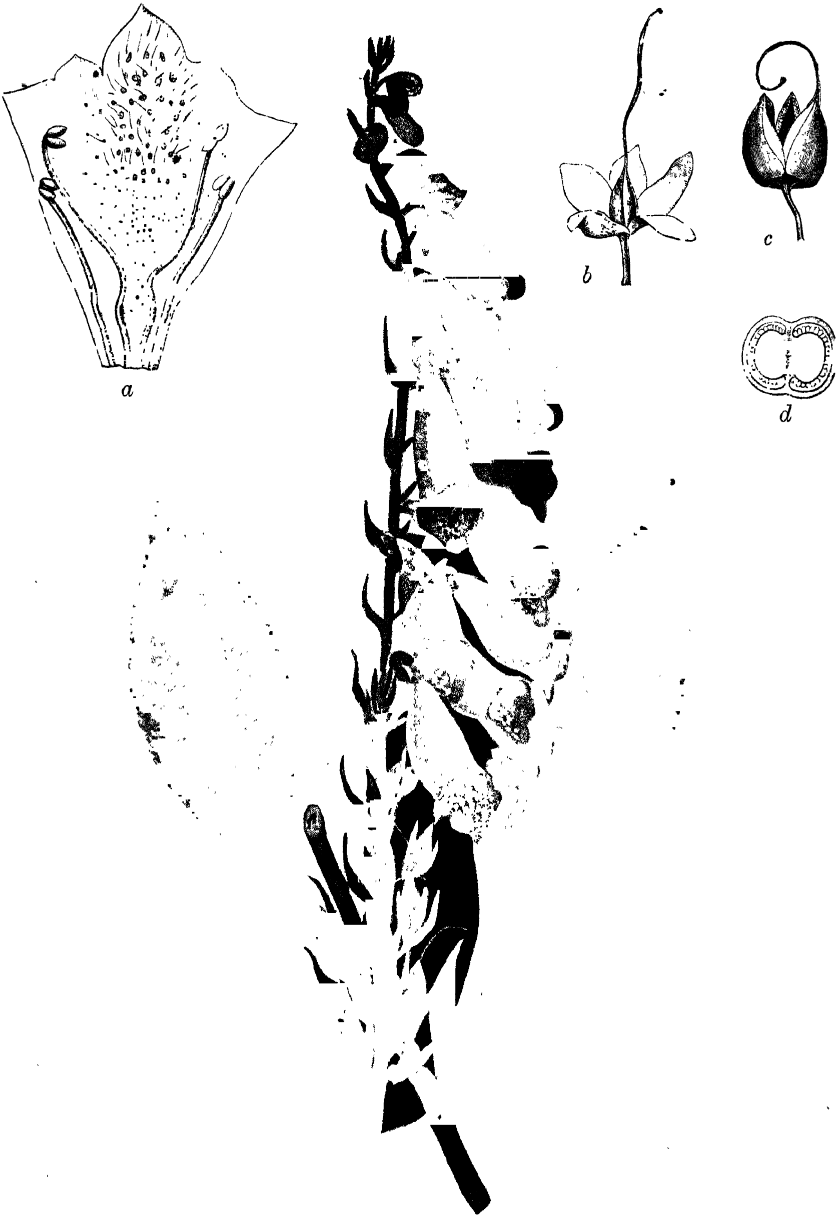


FIG. 791.—*Digitalis purpurea* (½ nat. size). *a*, Corolla cut open and spread out; *b*, calyx and pistil; *c*, fruit after dehiscence; *d*, transverse section of fruit (nat. size). POISONOUS.

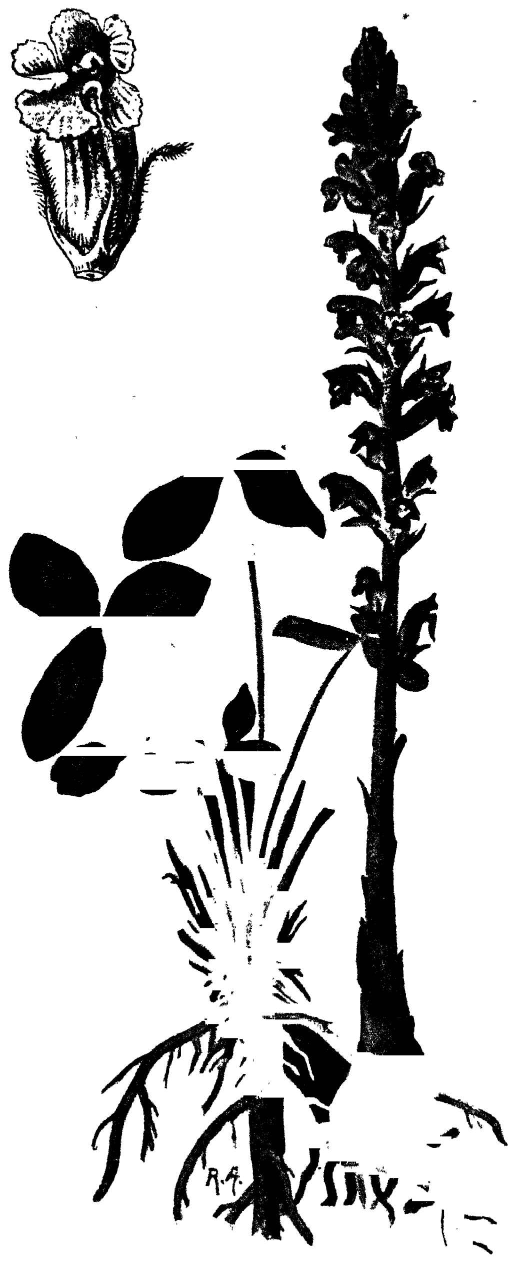


FIG. 792.—*Orobanche minor*, parasitic on *Trifolium repens* (½ nat. size). Single flower (enlarged).

In the tropics the Rubiaceae are abundantly represented by trees, shrubs, climbers, and epiphytes.

One of the most important Rubiaceae is *Cinchona*, a genus from the South American Andes, now cultivated in the mountains of nearly all tropical colonies (Fig. 793). Fruit, a capsule, with winged seeds (Fig. 794). *Coffea*, the Coffee plant, is a shrub; *C. arabica* (Fig. 795) and *C. liberica* are important economic plants, originally derived from Africa, and now cultivated throughout the tropics. The fruits are two-seeded drupes. The pericarp becomes differentiated into a succulent exocarp and a thin stony endocarp, which encloses the two seeds with their thin silvery seed-coats. These are the coffee-beans. The noteworthy tuberous epiphytic plants *Hydnophytum* and *Myrmecodia* (^{53}) have also succulent fruits; according to the most recent investigations they utilise the excreta of the ants which inhabit the cavities in the stems. Species of *Psychotria* and *Pavetta* (^{53a}) are also of physiological interest on account of the nitrogen-fixing bacteria harboured in their leaves. The association is more highly organised than that of the Leguminosae with the bacteria in their root-nodules, in that the bacteria here are present in the seeds and are thus handed on to a new generation.

OFFICIAL.—*Cinchona succirubra* yields CINCHONAE RUBRAE CORTEX. QUININE is obtained from this and other species of *Cinchona.* *Uragoga* (*Psychotria*) *Ipecacuanha* yields IPECACUANHA. *Coffea arabica* yields CAFFEINA.

Family 2. **Caprifoliaceae.**—Woody plants, usually without stipules. *Viburnum* has actinomorphic flowers with a trilocular ovary. The fruit contains only one seed. The sterile marginal flowers, which are alone represented in cultivated forms, serve as the attractive apparatus. *Sambucus,* Elder, has imparipinnate leaves, glandular stipules, and actinomorphic flowers. Zygomorphic flowers are found in the Honeysuckle (*Lonicera periclymenum*), one of our native lianes; the long-tubed, sweet-scented flowers are attractive to long-tongued Sphingidae. *Diervilla* (*Weigelia*) a favourite ornamental shrub.

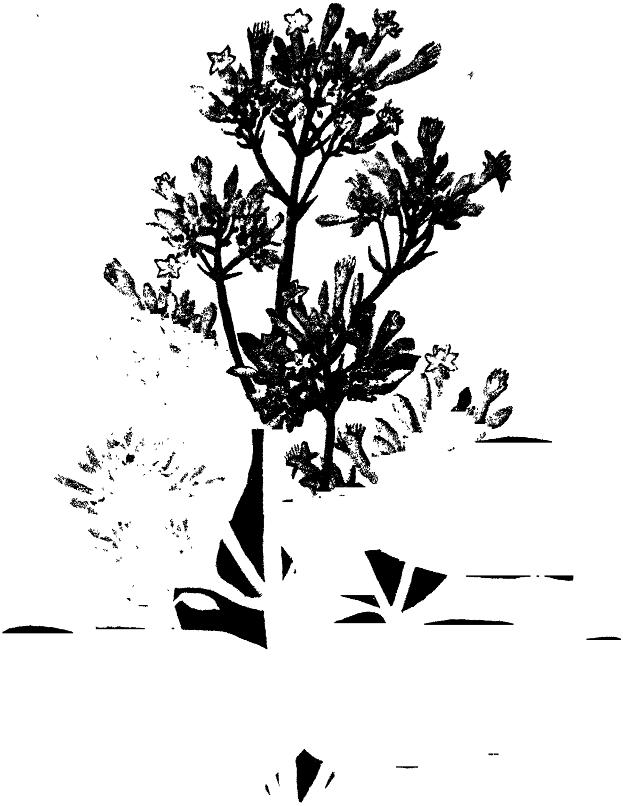


FIG. 793.—*Cinchona succirubra* (nat. size). (After SCHUMANN and ARTHUR MEYER.)

OFFICIAL.—*Viburnum prunifolium* yields VIBURNUM.

Family 3. **Valerianaceae.**—Herbs with decussately-arranged leaves and asymmetrical flowers. Calyx only developed on the fruit as a "pappus," *i.e.* a feathery crown assisting in wind-dispersal. *Valeriana*, the Valerian (Figs. 796, 797), has a spurred pentamerous corolla, three stamens, and three carpels, only one of which is fertile. Other Valerianaceae have only two (*Fedia*) or one (*Centranthus*) stamens in the flower.

OFFICIAL.—*Valeriana officinalis* yields VALERIANAE RHIZOMA. *V. Wallichii* yields VALERIANAE INDICAE RHIZOMA.

Family 4. **Dipsaceae.**—Herbaceous plants with opposite leaves and tetramerous or pentamerous actinomorphic or zygomorphic flowers. The individual flowers have an epicalyx which persists on the fruit and serves as a means of dispersal; they are associated in heads surrounded by sterile bracts.

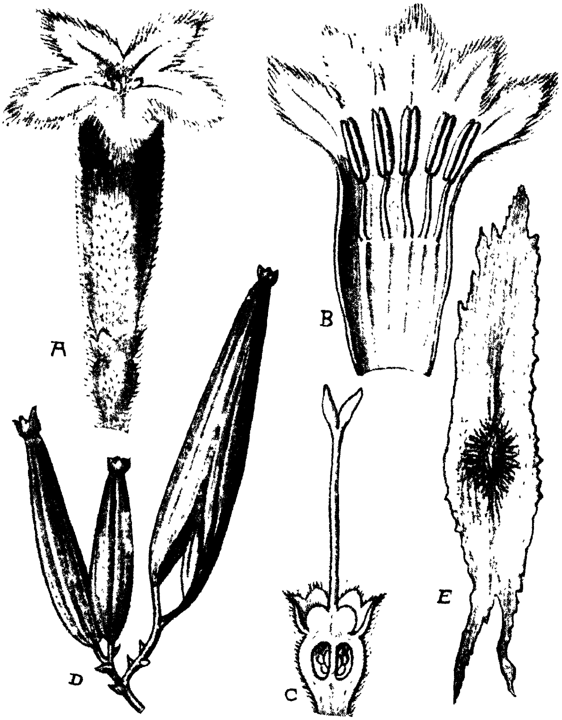


FIG. 794.—*Cinchona succirubra*. *A*, Flower. *B*, Corolla split open. *C*, Ovary in longitudinal section. *D*, Fruit. *E*, Seed. (*D* nat. size, the others enlarged.) (After A MEYER and SCHUMANN.)

Dipsacus, the Teazel, has recurved hooks on the involucral and floral bracts. Corolla with four lobes, four stamens, and one carpel containing a pendulous, anatropous ovule; endosperm present in the seed (Fig. 798). *Succisa* (Fig. 799) also has a four-lobed corolla; *Scabiosa* has a five-lobed corolla and the marginal flowers of the head are larger and dorsiventral. *Knautia* has tetramerous flowers; no floral bracts.

Order 28. Synandrae

The common character of this order is found in the fact that the anthers and sometimes the stamens in one way or another are fused or united together. The flowers may be actinomorphic or zygomorphic.

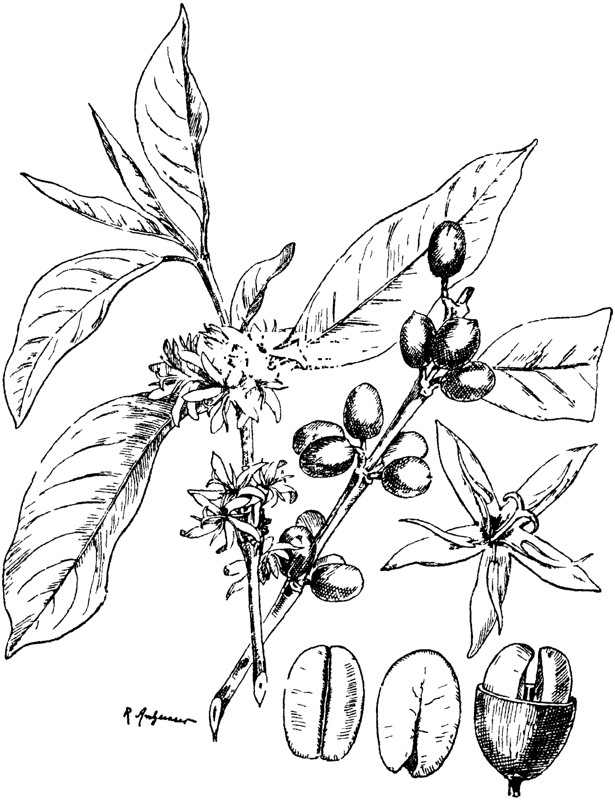


FIG. 795.—*Coffea arabica* ($\frac{1}{2}$ nat. size). Single flower, fruit, seed enclosed in endocarp, and free from it (about nat. size)

Family 1. **Cucurbitaceae.**—This family, in the frequently incomplete sympetaly it exhibits, shows a relationship to the Choripetalae, although to groups which have not been mentioned in this short survey. The other Sympetalae are, however, also connected with the Cucurbitaceae (see the phylogenetic table, p. 622). The Cucurbitaceae include herbaceous, coarsely hairy, large-leaved plants. Flowers diclinous; monoecious or less commonly dioecious. Calyx and corolla adherent below. Anthers united in pairs or all coherent; က-shaped (Fig. 800). Ovary trilocular (Fig. 800). Fruit, a berry, with a firm rind. The branched or unbranched tendrils correspond in their lateral position to bracts.

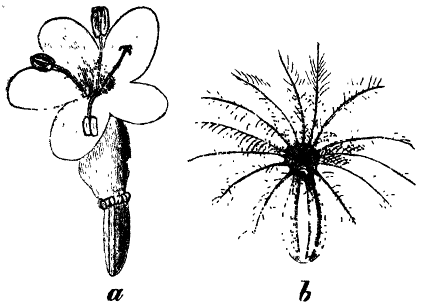


Fig. 796.—*Valeriana officinalis.* *a*, Flower (× 8); *b*, fruit (enlarged).

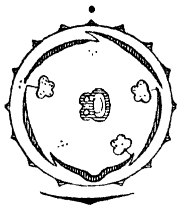


Fig. 797.—*Valeriana.* Floral diagram. (After Noll.)

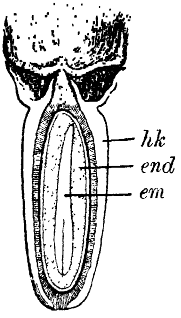


Fig. 798.—Fruit of *Dipsacus fullonum* in longitudinal section. *hk*, Calyx tube; *end*, endosperm; *em*, embryo. (After Baillon.)

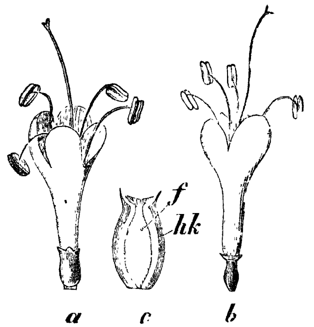


Fig. 799.—*Succisa pratensis.* *a*, Flower with epicalyx; *b*, the same after removal of epicalyx; *c*, fruit in longitudinal section; *f*, ovary; *hk*, epicalyx. (After H. Schenck.)

Cucumis sativus, the Cucumber, and ***Cucumis Melo***, the Melon, are commonly cultivated. The Cucumber is parthenocarpic (54), *i.e.* pollination of the stigma is not necessary for the setting of the fruit. *Cucurbita Pepo*, the Pumpkin. *Bryonia*, Bryony. *Citrullus Colocynthis* is a perennial plant of subtropical deserts. Leaves deeply three-lobed and pinnately divided. Tendrils simple or forked; male and female flowers solitary in the axils of the leaves. The fruit is a dry berry (Fig. 801).

Official.—*Citrullus Colocynthis* yields colocynthidis pulpa. *Cucurbita maxima* yields cucurbitae semina.

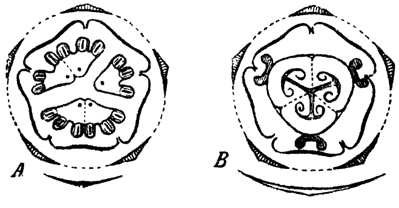


Fig. 800.—*Ecballium* (Cucurbitaceae). Diagrams of (*A*) a male and of (*B*) a female flower. (After Eichler.)

The association of the following families with the Cucurbitaceae is only possible on the morphological character afforded by the united anthers. A real relationship appears improbable, especially since the investigations of KRATZER have shown how various is the course of development of the seeds.

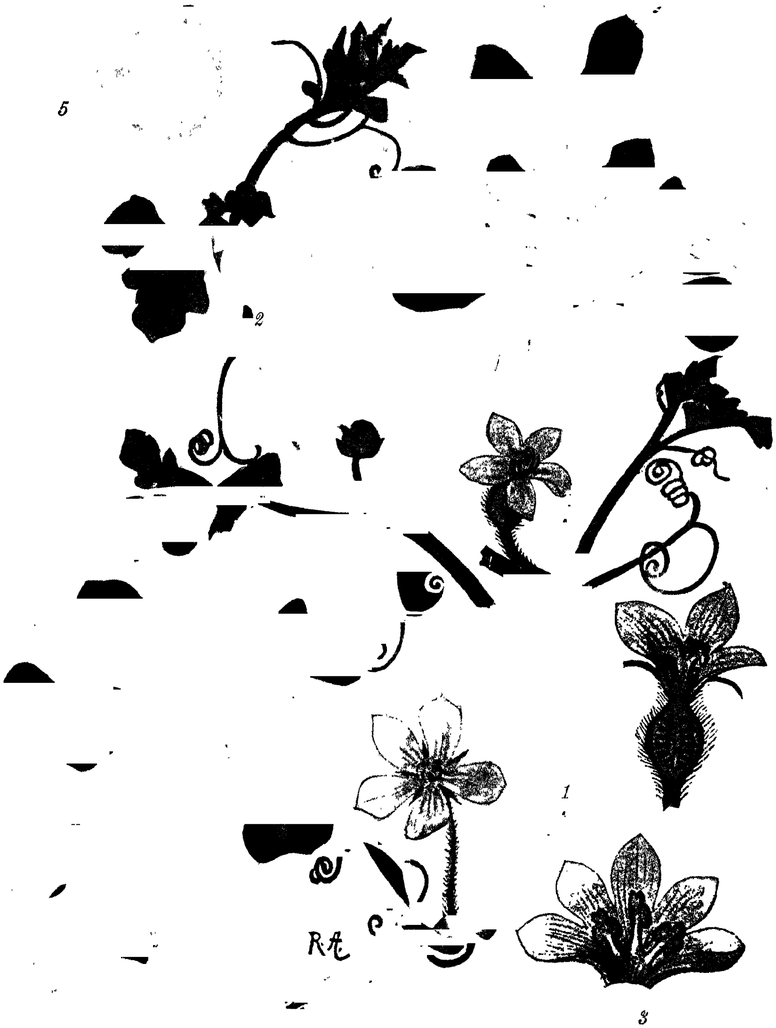


FIG. 801.—*Citrullus Colocynthis* (½ nat. size). *1*, Shoot with male and female flowers. *2*, Apex of a shoot with a male flower-bud and tendrils. *3*, Male flower with corolla spread out. *4*, Female flower cut through longitudinally. *5*, Young fruit cut transversely.

Family 2. **Campanulaceae.**—Herbs with milky juice; flowers actinomorphic; ovary as a rule trilocular or pentalocular. The stamens are inserted on the floral axis and have their anthers joined together. The genus *Campanula* (Figs. 802, 803) has a number of British species with blue bell-shaped flowers. *Phyteuma* has spike-like inflorescences, the petals only separate near the base. Only after the pollen, which has been shed in the bud, has been swept out by the hairs on the style (55) do the petals open and the arms of the stigma spread apart. *Jasione* has capitulate inflorescences resembling those of Compositae.

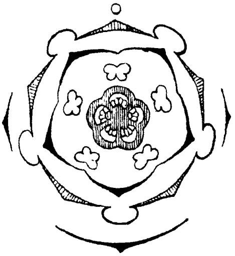


FIG. 802.—Floral diagram of *Campanula medium*. (After EICHLER.)

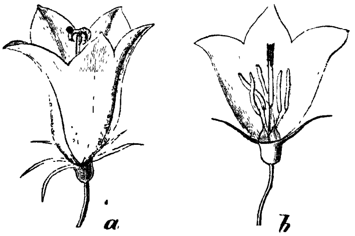


FIG. 803.—*Campanula rotundifolia*. *a*, Flower; *b*, the same cut through longitudinally. (Nat. size.) (After H. SCHENCK.)

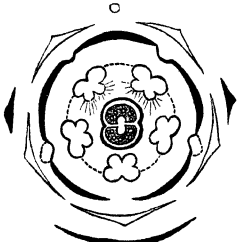


FIG. 804.—Floral diagram of *Lobelia fulgens*. (After EICHLER.)

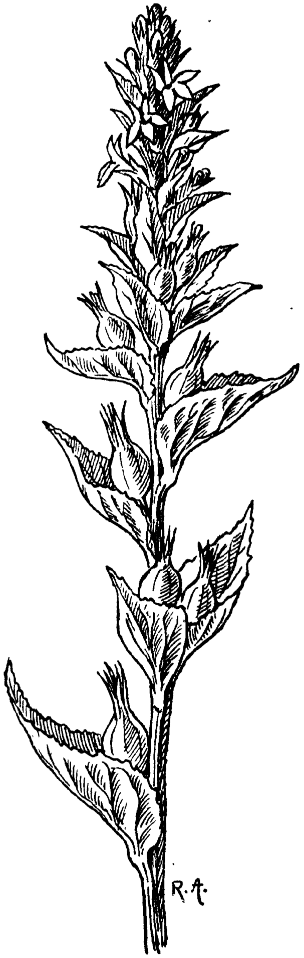


FIG. 805.—*Lobelia inflata*. Upper portion of plant with flowers and fruits.

Family 3. **Lobeliaceae** differ from the Campanulaceae in the zygomorphic flowers and two carpels. The median sepal is anterior and comes below a deep incision in the corolla. The normal position is assumed by torsion of the whole flower through 180° or inversion of the flower (Figs. 804, 805). In Britain

Lobelia Dortmanna, an aquatic plant of northern regions, has a similar habit to *Litorella* (56).

OFFICIAL.—*Lobelia inflata* from North America (Fig. 805) yields LOBELIA.

Family 4. Compositae (57).—Distributed over the whole earth. For the most part herbs of very various habit; some tropical forms are shrubs or trees, *e.g. Senecio Johnstoni*, *S. adnivalis* (Fig. 814). The flowers are associated in heads and are either all alike or of different types in the head. The single flowers are actinomorphic or zygomorphic. Stamens five; anthers introrse, cohering by their cuticles to form a tube (Fig 806) which is closed below by the unexpanded stigma. The flowers are protandrous; the pollen is shed into the tube formed by the anthers and is swept out by the brush-like hairs of the style as the latter elongates. The style is bifid above, forming

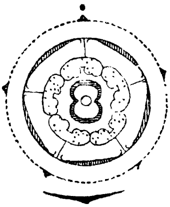


Fig. 806.—Compositae. Floral diagram (*Carduus*).

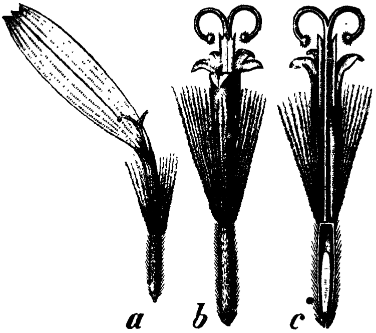


Fig. 807.—*Arnica montana*. *a*, Ray-flower; *b*, disc-flower; *c*, the latter cut through longitudinally. (After Berg and Schmidt, magnified.)

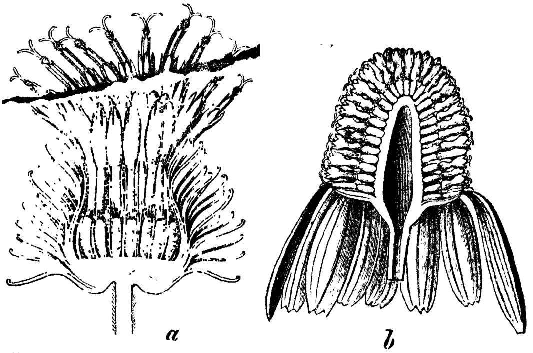
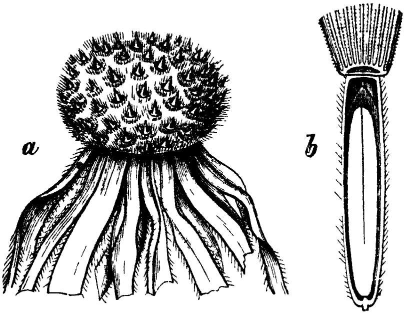


Fig. 808.—Longitudinal section of capitulum—*a*, of *Lappa major* with hooks on the involucral bracts and with floral bracts; *b*, of *Matricaria Chamomilla* without floral bracts. (After Berg and Schmidt, magnified.)

the stigma. Ovule erect, anatropous (Fig. 809). Seed exalbuminous. The fruits often bear at the upper end a crown of hairs, the pappus. This corresponds to the calyx and aids in the dispersion of the fruit by the wind (Fig. 807). As a reserve-material in roots and tubers (Fig. 198) inulin as a rule is found; in the seeds aleurone grains and fatty oil.

The individual flowers are either radially symmetrical with a five-lobed corolla (Fig. 807, *b*, *c*) or they are two-lipped as in the South American Mutisieae, the upper lip having two teeth, the lower three. By suppression of the upper lip, flowers with a single lip are derived; such flowers exhibit three teeth at the tip (Fig. 807 *a*). The ligulate flowers (*e.g.* of *Taraxacum*) are similar in general appearance to the latter; the corolla is here deeply split on one side and its margin bears five teeth. In addition to those Compositae which have only ligulate or only tubular florets in the head, there are many which have tubular florets disc-florets) in the centre, surrounded by one-lipped florets (ray-florets). These



[illegible] *Arnica montana.* *a*, Receptacle of capitulum after remov[illegible] *b*, fruit in longitudinal section, the pappus only partly shown. (After BERG and SCHMIDT, magnified.)

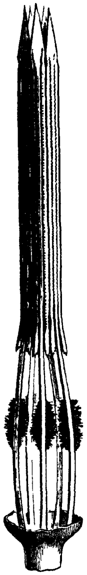


FIG. 810.—Androecium of *Carduus crispus* (× 10). (After BAILLON.)

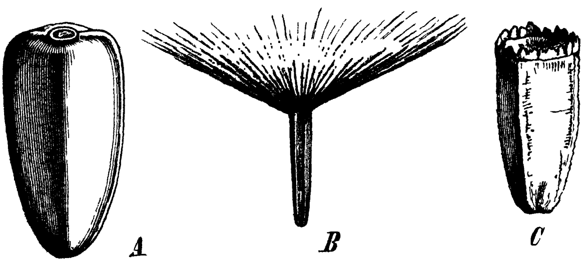


FIG. 811.—Fruits of—*A*, *Helianthus annuus*, *B*, *Hieracium virosum*, *C*, *Cichorium Intybus*. (After BAILLON.)

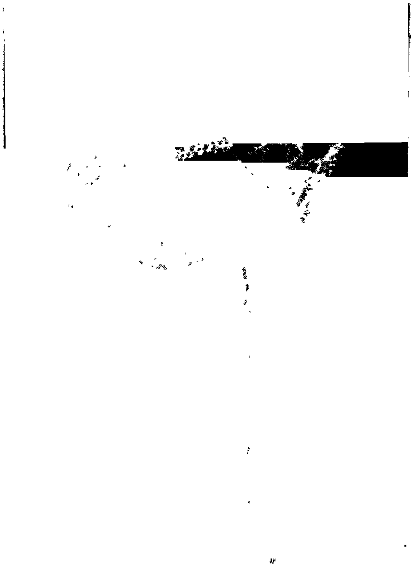


Fig. 812.—Head of fruits of *Taraxacum officinale.* The pappus is raised above the fruit on an elongated stalk. (Nat. size.)

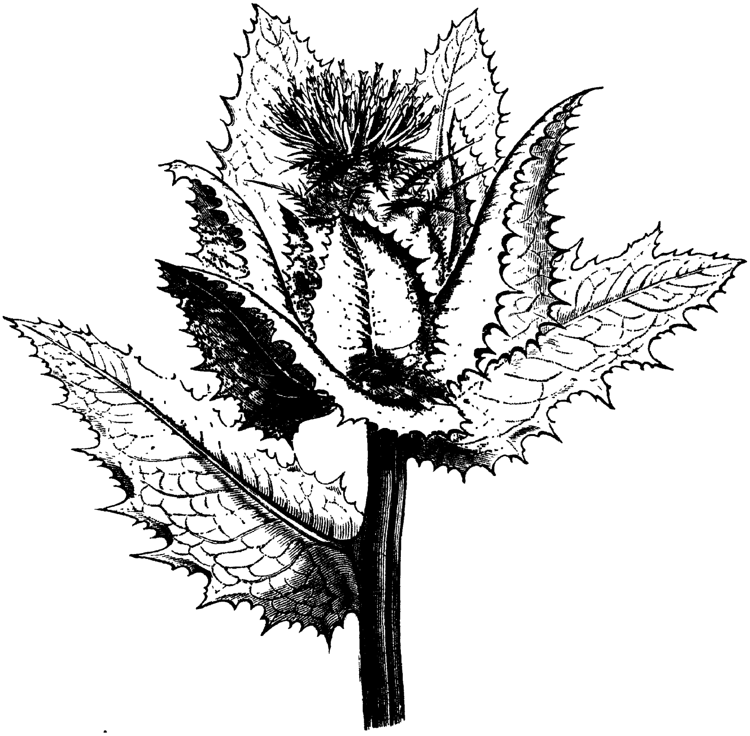


Fig. 813.—*Cnicus benedictus.* (After Baillon.)

usually differ from one another in sex as well as in colour; the disc-florets are hermaphrodite, the ray-florets purely female. The flower-heads are thus heterogamous (*Matricaria*, *Arnica*). Lastly, the marginal florets may be completely sterile (*Centaurea cyanus*) and serve only to render the capitulum conspicuous to insects.

One series of genera has only tubular florets in the head. *Carduus* (Plumeless Thistle), pappus of simple, hair-like bristles (Fig. 810). *Cirsium*, with feathery pappus. *Echinops*, with single-flowered capitula associated in numbers. *Lappa* (Burdock), (Fig. 808 *a*), involucral bracts with recurved, hook-like tips. *Cynara Scolymus* (Artichoke). *Cnicus benedictus* (Fig. 813), capitula solitary, terminal, surrounded by foliage-leaves. Involucral bracts with a large, sometimes pinnate, terminal spine and a felt of hairs. *Centaurea* with dry, scaly, involucral bracts and large, sterile, marginal florets.

FIG. 814.—*Senecio keniadendron* from the Upper Alpine region of West Kenya (East Africa). (After ROB. E. FRIES.)

Other genera have only hermaphrodite ligulate florets in the capitulum, and have latex in all parts of the plant. *Taraxacum officinale* (Dandelion) is a common plant throughout the northern hemisphere. It has a long tap-root, a rosette of coarsely-toothed leaves, and inflorescences, borne singly on hollow stalks; after flowering these exhibit a second period of growth (p. 282, Fig. 254). Fruits with an elongated beak, carrying up the pappus as a stalked, umbrella-shaped crown of hairs (Fig. 812). *Lactuca sativa*, Lettuce. *L. virosa*. *L. Scariola*, Compass plant, has leaves which take a vertical position (cf. p. 353). *Cichorium Intybus* (Chicory) has blue flowers and a pappus in the form of short, erect scales (Fig. 811 *C*). *C. endivia*, Endive. *Tragopogon* and *Scorzonera* have a feathery pappus ; *Sc. hispanica*. *Crepis* has a soft, flexible, hairy pappus of

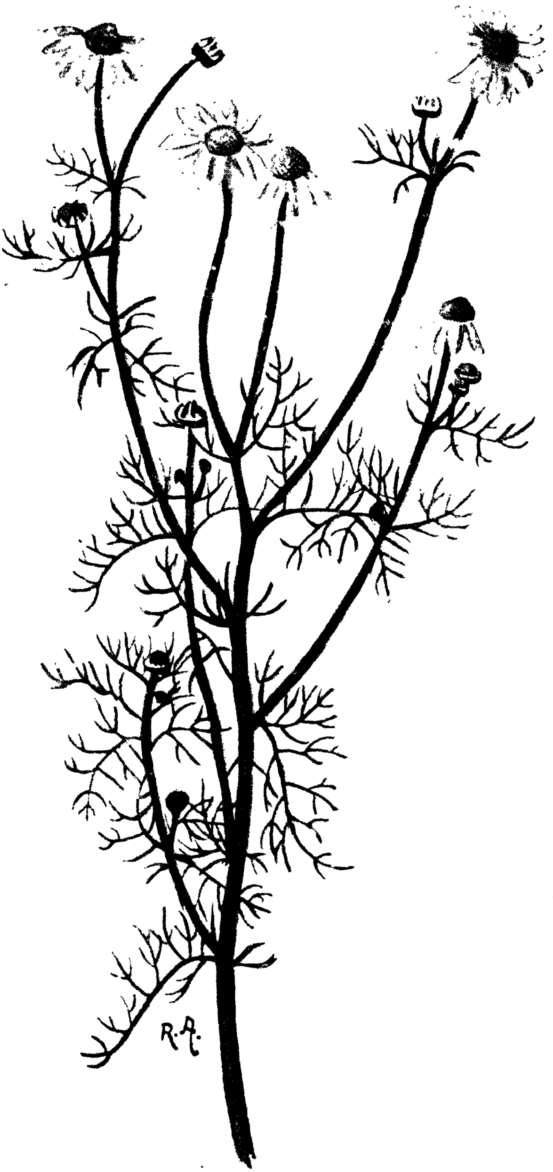


FIG. 815.—*Matricaria Chamomilla* (⅔ nat. size).

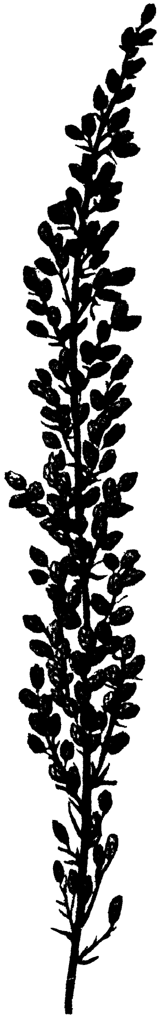


FIG. 816.—*Artemisia Cina*. (After SCHUMANN and ARTHUR MEYER.)

brownish colour. *Sonchus*, pappus of several series of bristles. *Hieracium*, a large European genus with many forms. Pappus white, rigid, and brittle (Fig. 811 *B*).

Usually there are florets of two distinct types in the capitulum. Numerous species of *Aster*, *Solidago*, and *Erigeron* occur in Europe, America, and Asia. Species of *Aster* are cultivated. Species of *Haastia* and *Raoulia* are cushion-shaped plants with woolly hairs in New Zealand (Vegetable Sheep) (Fig. 184).

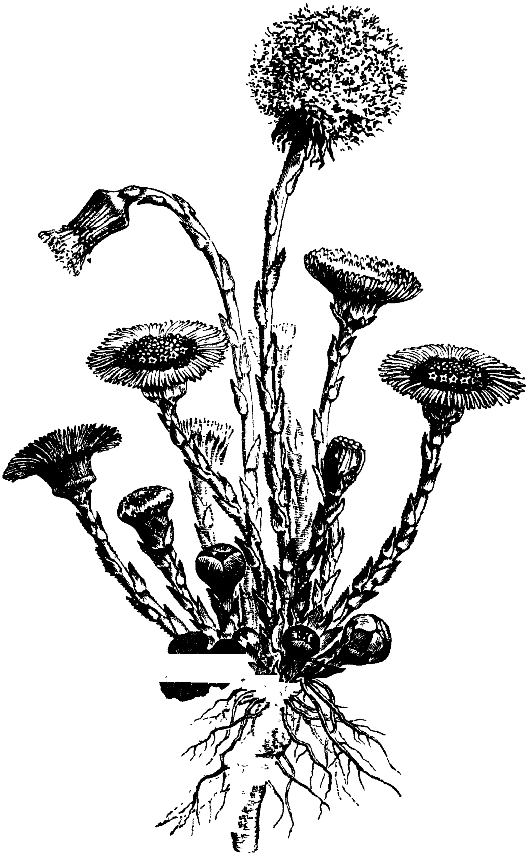


FIG. 817.—*Tussilago Farfara.* (After BAILLON.)

Inula occurs in Britain; involucral leaves frequently dry and membranous. In *Gnaphalium*, *Antennaria*, *Helichrysum* (Everlasting flowers), *Leontopodium* (Edelweiss), *Filago*, etc., the dry involucral bracts are coloured. *Helianthus annuus* (Sunflower, Fig. 811 *A*), cultivated for its oily fruits, *H. tuberosus* (Jerusalem Artichoke), with edible tubers. *Dahlia*, from America and in cultivation. In Britain; *Bidens*, herbs with opposite leaves, sometimes heterophyllous. *Achillea*, Milfoil; *A. moschata* and *A. atrata* are corresponding species of the Alps, the one on limestone and the other on schists. *Anthemis nobilis*, capitula composed of disc-florets only, or with these more or less replaced by irregular florets. *Anacyclus officinarum. Matricaria Chamomilla* (Chamomile, Figs. 808, 815) is an annual copiously-branched herb with a hollow, conical, common receptacle, yellow disc-florets and white, recurved, female ray-florets, in the terminal capitula. *Chrysanthemum, C. segetum. Tanacetum*, flowers all tubular, marginal florets female. *Artemisia* has all the florets tubular and usually the peripheral ones female (*A. Absinthium*, Wormwood); in the few-flowered capitula of *A. Cina* (Fig 816) all the florets are hermaphrodite.

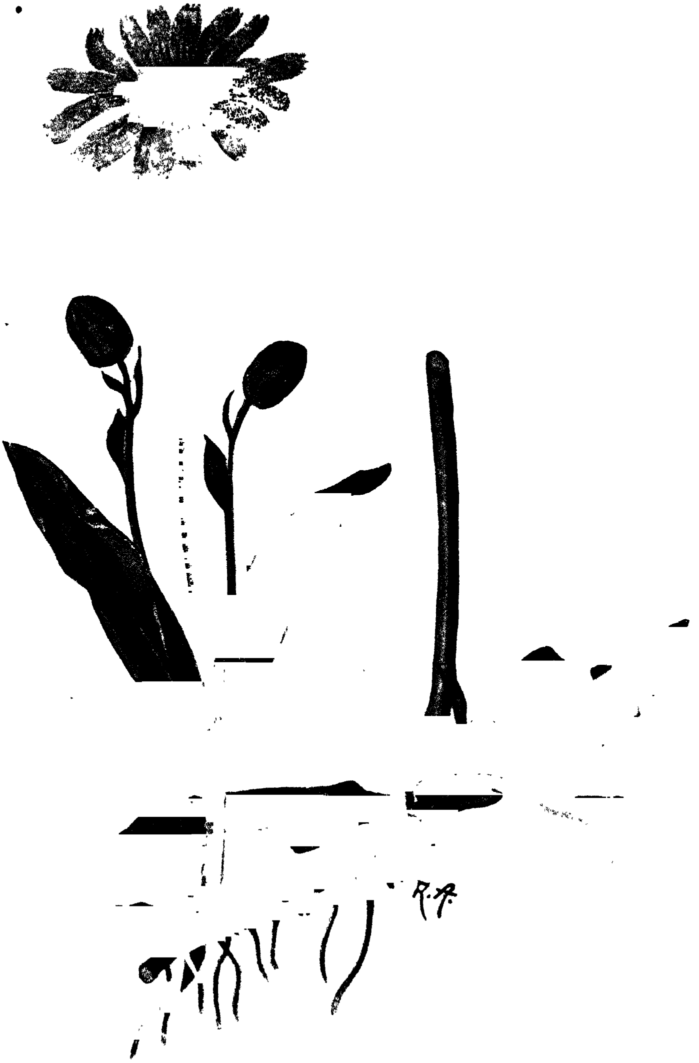


FIG. 818.—*Arnica montana* (½ nat. size).

Tussilago Farfara, Coltsfoot, flowers appear before the leaves; the flowering stem bears scaly leaves and a single capitulum (Fig. 817); the flowers stand on a smooth receptacle and have a fine, white, hairy pappus. Female flowers at the periphery in several series. Leaves large, cordate, thick, covered beneath with white hairs. *Petasites officinalis*, Butter-Bur. *Senecio*, plants of diverse habit, including some trees and succulent plants; of world-wide distribution. Dendroid species of *Senecio* occur on the volcanic mountains of Central and East Africa (Fig. 814). *S. vulgaris* has no ray-florets but only tubular, hermaphrodite florets. *Doronicum*, *Cineraria* are commonly cultivated. *Arnica montana* (Figs. 807, 809, 818) has a rosette of radical leaves in two to four opposite pairs and a terminal inflorescence bearing a single capitulum; from the axillary buds of the two opposite bracts one (rarely more) lateral inflorescence develops. *Calendula* and *Dimorphotheca* have the fruits of the capitulum of varied and irregular shapes.

Official.—*Anacyclus Pyrethrum* yields PYRETHRI RADIX. Santoninum is prepared from *Artemisia maritima*, var. *Stechmanniana*. *Anthemis nobilis* yields ANTHEMIDIS FLORES. *Taraxacum officinale*, TARAXACI RADIX. *Arnica montana*, ARNICAE FLORES. *Grindelia camporum*, GRINDELIA.

Sub-Class II

Monocotylae

The derivation of the Monocotyledons from the Dicotyledons must, as has already been stated, be sought in the Polycarpicae. As regards general habit, the herbaceous Ranales come closest to the Monocotyledons which are, as a rule, herbaceous plants. Ecologically the lowest Monocotyledons are water-plants like the Nymphaeaceae among the Polycarpicae. Secondary thickening is wanting in the herbaceous Polycarpicae as in Monocotyledons. Trimerous flowers occur in the Lauraceae, Berberidaceae, and Nymphaeaceae, and throughout the Monocotyledons; the apocarpous gynaeceum of Polycarpicae appears in the Alismataceae and Butomaceae among the Helobiae. There is thus no one family of the Polycarpicae from which the Monocotyledons can be regarded as derived. It is the general organisation of the order which is significant. This is supported by the detailed comparison of the nectaries of the flowers made by Porsch (^{58}). Serologically also the relationship of the Polycarpicae with the Monocotyledons and in particular with the Helobiae is confirmed.

The Monocotyledons, or Angiosperms which possess a single cotyledon, are in general habit mostly herbaceous, less frequently shrubs or trees. In germination the radicle and hypocotyl of the small embryo emerge from the seed-coat, while the sheath-like cotyledon usually remains with its upper end within the seed (Fig. 616 *b*) and absorbs the materials stored in the endosperm, which is usually well developed. The growth of the main root is sooner or later arrested and its place taken by numerous adventitious roots springing from the stem. In the Grasses these are already present in the embryo within the seed. Thus a single root-system derived by the branching of a main root, such as the Gymnosperms and Dicotyledons possess, is wanting throughout the Monocotyledons.

The laterally placed growing point of the stem (Fig. 596) remains for a longer or shorter time enclosed by the sheath of the cotyledon. Later it bears in two-ranked or alternate arrangement the leaves, which have long sheaths and continue to grow for a considerable time at their bases. The growth of the stem is often limited; branching is in many cases entirely wanting, and rarely results in the development of a highly branched shoot-system. The leaves are mostly sessile and parallel-veined, and of a narrow, elongated, linear, or elliptical shape (Fig. 819). The pinnate or palmate leaves of the Palms and the perforated leaves of some Araceae are due to the perishing of definite portions of the lamina during development.

Anatomically the Monocotyledons are characterised by their closed vascular bundles in which no cambium is developed; these are uniformly scattered in the cross-section of the stem (cf. Fig. 105). Secondary thickening is consequently wanting in Monocotyledons, and in the rare cases in which it is found results from the formation at the periphery of the central cylinder of additional closed bundles embedded in ground-tissue.

The flower in the Monocotyledons is usually pentacyclic and has two whorls constituting the perianth, an androecium of two whorls, and a gynaeceum of a single whorl. The typical number of members in each whorl is three. The two whorls of the perianth are usually similarly formed, and thus constitute a perigone (Fig. 547). The floral formula of such a flower is P 3 + 3, A 3 + 3, G (3).

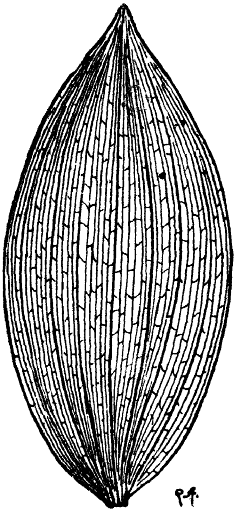


FIG. 819.—Leaf of *Polygonatum multiflorum* with parallel venation (⅔ nat. size).

(a) Flowers usually complete, pentacyclic and actinomorphic

Order 1. Helobiae

This order includes only aquatic or marsh-plants. The radial or actinomorphic flowers have the gynaeceum frequently apocarpous and composed of two whorls of carpels, which develop into indehiscent fruitlets or follicles. Seeds exalbuminous; embryo large. The order connects by its floral structure the Monocotyledons with the Polycarpicae.

Family 1. **Alismataceae.**—Widely spread in the warm and temperate zones. *Alisma Plantago*, *Sagittaria sagittifolia*, and *Butomus umbellatus* have long-stalked panicles or umbels, and occur as marsh-plants. The individual flowers have a calyx and a white (in *Butomus*, reddish) corolla. Androecium, with six or more stamens. Gynaeceum apocarpous, with six or many carpels that may be in whorls or spirally arranged (Fig. 820). *Sagittaria* is monoecious with flowers that, by suppression of stamens or carpels, are unisexual. Male flowers, with numerous stamens and sterile carpels ; female flowers, with staminodes and numerous free carpels inserted on the convex floral receptacle (Fig. 821). Leaves in *Butomus*, linear, channelled, and triangular in cross-section ; in *Alisma* and *Sagittaria*, long-stalked with spoon-shaped and sagittate leaf-blades respectively. Individuals of both genera growing in deep-flowing water have long ribbon-shaped leaves, similar to those that appear as a transition type in germination ; such plants do not flower.

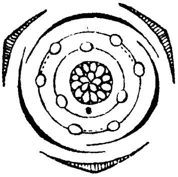


FIG. 820. —Floral diagram of *Echinodorus parvulus*, one of the Alismataceae. (After EICHLER.)

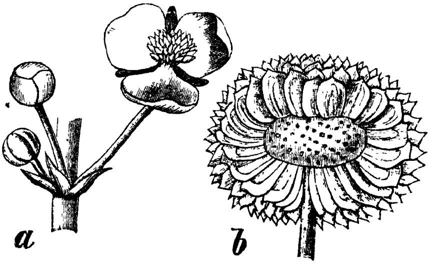


FIG. 821. —*Sagittaria sagittifolia*. *a*, Flower; *b*, fruit after removal of some of the carpels. (Magnified; *b*, after ENGLER and PRANTL.)

Family 2. **Potamogetonaceae.**—Many species of *Potamogeton* are distributed over the earth in standing or flowing water. Leaves usually submerged, with a long sheath, slit on one side, formed from the axillary stipules. *P. natans*, the common Pond-weed (Fig. 822), at the time of flowering has usually only floating leaves, the cylindrical, submerged water-leaves having disappeared by then. *Ruppia maritima* and *Zanichellia palustris* grow in brackish water. *Zostera marina*, Grass-wrack, occurs commonly on all north temperate coasts and is used for stuffing cushions.

Family 3. **Naiadaceae.** *Naias marina*, dioecious, ♂ fls. with a single stamen ; ♀ with one carpel in a cup-shaped investment.

Family 4. **Hydrocharitaceae.** –*Hydrocharis morsus ranae* and *Stratiotes aloides* are floating plants occurring in Britain, which are vegetatively propagated by runners ; they pass the winter at the bottom of the water, in some cases as special winter buds, and grow up again in the spring. Flowers dioecious ; entomophilous. The male flower has several trimerous whorls of stamens ; the female flower possesses staminodes and two trimerous whorls of carpels. *Vallisneria spiralis*, a fresh-water plant of the tropics extending to the Italian lakes. *Elodea canadensis*, the Canadian water-weed, now widely distributed (hydrophilous, cf. p. 564).

Order 2. Spadiciflorae

The common character of this order is afforded by the peculiar inflorescence ; this is a spike with a thick, swollen, often fleshy axis and is termed a spadix. The flowers are mostly diclinous, monoecious, or more rarely dioecious.

Family 1. **Typhaceae.**—Marsh-plants, with long, linear leaves and long-stalked spikes, which bear a large number of flowers, the male above, the female lower down. Perianth wanting.

Family 2. **Sparganiaceae.**—Connected with the preceding family. Spikes spherical. Flowers with a perigone, but otherwise like the Typhaceae.

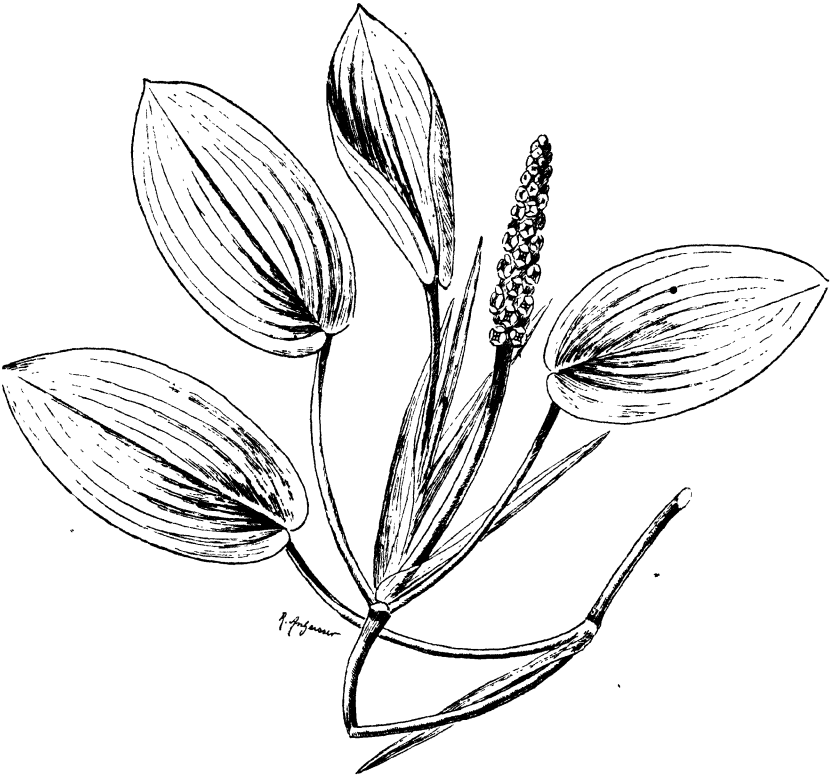


Fig. 822.—*Potamogeton natans.* Flowering shoot. (½ nat. size.)

Family 3. **Pandanaceae.**—Screw-pines. Trees of peculiar appearance, supported by prop-roots, or climbing shrubby plants; all belong to the tropical countries around the Indian Ocean and to the Pacific islands. Leaves elongated, spiny, channelled above, arranged without bare internodes in three spiral ranks on the axis (58a). Inflorescences, ♂ or ♀, are terminal spikes in the axils of sheathing bracts. Flowers without perianth, *Pandanus* (cf. Fig. 825 in front of the Palms), *Freycinetia* scrambling climber.

Family 4. **Palmae** (59).—The Palms are an exclusively tropical and subtropical family, the members of which mostly attain the size of trees. Their slender stem is simple and usually of uniform diameter throughout; only the African species of *Hyphaene* have branched stems.

Other forms show evident growth in thickness towards the base and sometimes for half the height of the stem; this depends on enlargement of the elements already present. The Pandanaceae behave similarly. The leaves, which are often of gigantic size, form a terminal crown. They are either pinnately or palmately divided, the division coming about by the death of definite portions of tissue in the young leaf in the bud, and subsequent tearing along these lines. The inflorescence is in some cases terminal (*Metroxylon*), and the individual perishes with the development of the fruits. More often the inflorescences are axillary. When young, they are enclosed by a massive resistant sheath, the spathe; this bursts open and permits of the unfolding of the simple, or more usually branched, inflorescence (Fig. 823).

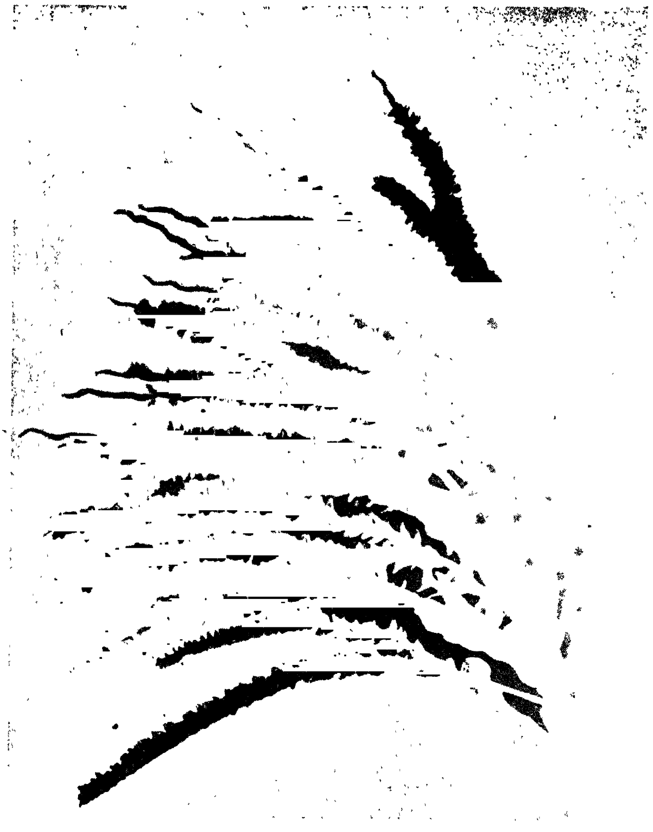


FIG. 823.—*Cocos nucifera*. Inflorescence of the Coco-nut Palm. (Greatly reduced.)

The individual flowers are as a rule unisexual and constructed on the ordinary monocotyledonous type; P 3 + 3, A 3 + 3, in the male flowers, and P 3 + 3, G (3), in the female flowers. In *Cocos* their distribution is monoecious. Fig. 823 represents the inflorescence of *Cocos nucifera*, still partly enclosed by the spathe. The male flowers are crowded on the terminal branches of the inflorescence, while the female flowers are considerably larger and stand singly lower down. The ovary, which is here composed of three united carpels, becomes, as a rule, unilocular in the fruit, since only one carpel develops further. The ripe fruits are borne in small numbers on each inflorescence. Each has a smooth exocarp, a fibrous mesocarp, which contributes to the buoyancy of the fruit in water and thus leads to the wide distribution of this palm on tropical coasts, and a hard endocarp. At the base of each carpel a germinal pore is present in the endocarp (Fig. 824), but only the one in relation to which the embryo lies remains permeable. The endosperm forms a thick layer within the endocarp; it is rich in fatty substances and produces the COPRA of commerce. The space within the endosperm is partially filled with fluid, the "milk" of the coco-nut, which is possibly of service in germination. The embryo on germination develops a massive absorbent organ which grows into the cavity of the fruit and serves to absorb the reserve-materials. Fig. 825 shows the general habit of Coco-nut palms.

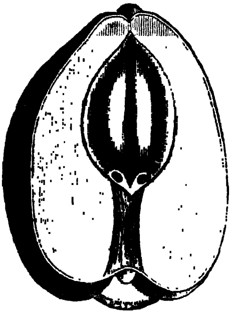


FIG. 824.—Coco-nut after partial removal of the fibrous mesocarp. (Reduced. After WARMING.)

In *Areca catechu* (Fig. 851) the fruit developed from a similar ovary to that of *Cocos* is a berry, the mesocarp becoming partly fibrous and partly succulent. The white endosperm is here of stony consistence, cellulose being stored as a reserve-material; the endosperm is ruminated, *i.e.* the dark seed-coat grows into it at many points and gives it a veined appearance. The fruit of the Date Palm (*Phoenix dactylifera*) is also a berry, but this arises from one of the carpels of the apocarpous gynaeceum, the other two not developing. In contrast to the other genera mentioned, *Phoenix* is dioecious. Other important economic plants among the Palms are *Elaeïs guineensis*, the African Oil Palm, species of *Calamus* which yield Malacca Cane, and species of *Metroxylon*, from which Sago is obtained; the two latter are found in the Asiatic-Australian region of the tropics. *Phytelephas macrocarpa*, an American Palm which does not form a trunk, yields VEGETABLE IVORY (the hard endosperm). Several species yield a flow of sugary sap on cutting off the inflorescence, and this is sometimes fermented to make Palm-wine and sometimes used as a source of cane-sugar (*Arenga saccharifera*).

Family 5. **Araceae.**—The Araceae are mostly herbs or shrubs; they take a conspicuous place as root-climbers in the damp, tropical forests (Fig. 826). The leaves of some species (*e.g. Monstera*) have the large lamina incised or perforated; this comes about by the death of definitely limited areas and is comparable to the method by which the leaves of Palms become compound. The flowers are greatly reduced, usually diclinous, borne on a swollen, fleshy axis; a spathe, often of bright colour and serving to render the inflorescence conspicuous, is present at the base of the spike (*e.g. Anthurium scherzerianum*, *Richardia aethiopica*, both of which are commonly cultivated). Fruit usually a red, bluish, or white berry. *Colocasia* (see p. 232) and *Caladium* are frequently cultivated on account of their large, beautifully coloured leaves. *Ariopsis* and *Spathicarpa* have characteristic inflorescences.

FIG. 825.—Coco-nut Palms at Hilo, Hawaii. *Pandanus odoratissimus* in front of the Palms.

Acorus calamus has, in the course of the last two or three centuries, spread to this country from the East. It has complete, hermaphrodite flowers; ovary trilocular. The short spadix is terminal, but is displaced to one side by the spathe, which resembles the foliage-leaves (Fig. 827).

POISONOUS.—Many Araceae are poisonous. *Calla palustris* in peaty swamps. *Arum maculatum* (Fig. 828), a perennial herb with tuberous rhizome, common in woods. It develops a number of stalked, hastate leaves, the brown spots on which give the plant its specific name. The flowers are monoecious, without perianth, the female flowers stand at the base of the spadix and the male a short distance above them. Above the latter come a number of sterile flowers with downwardly directed, hair-like points, which stand at the level of the constricted portion of the spathe; this is widely open above. Pollination, see p. 567.

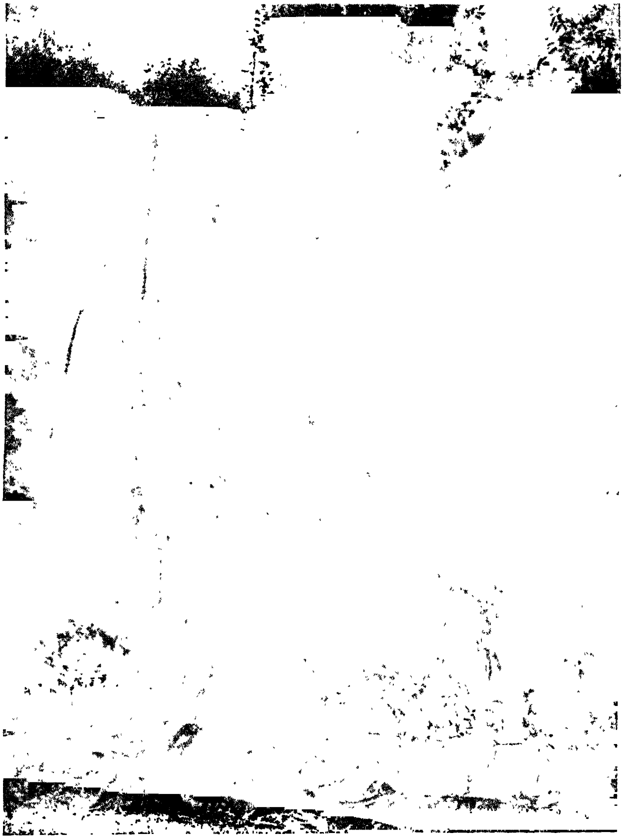


FIG. 826.—Root-climbing Araceae in the moist tropical forest of Chiapas (Cafetal Trionfo). From the examples above the region figured rope-like roots hang down to the ground. They serve to nourish the plant after the death of the stem.

Order 3. Liliiflorae

Flowers actinomorphic, composed of five whorls, with superior or inferior ovary (Fig. 547). Both whorls of the perianth developed alike. Only in the Iridaceae is one whorl of the androecium suppressed. The gynaeceum varies in position, but it is always formed of three carpels and in most cases has a trilocular ovary.

Family 1. Juncaceae.—Plants of grass-like habit. Flower of complete Liliaceous type; with scaly perianth. Wind-pollination. Pollen-grains united in tetrads. Ovary superior, uni- or tri-locular, bearing three long papillose stigmas. Endosperm floury. Fruit a capsule. Distributed in the temperate zones of both hemispheres.

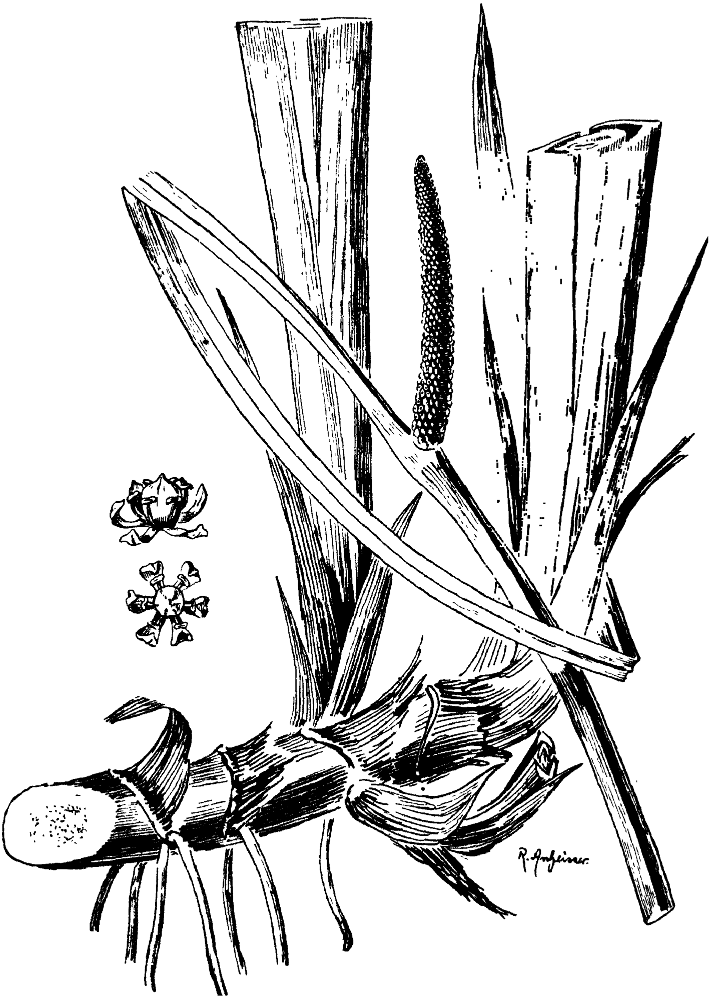


Fig. 827.—*Acorus calamus.* Flowering plant. Single flowers seen from above and from the side. (½ nat. size.)

Numerous species of *Juncus* (Rush) occur in our flora, in marshy ground; the leaves are cylindrical and have large, intercellular spaces. The clusters of small anemophilous flowers (Fig. 829) are borne on the end of a shoot, but are often displaced to the side by the bract which continues the line of the axis. Fruits with

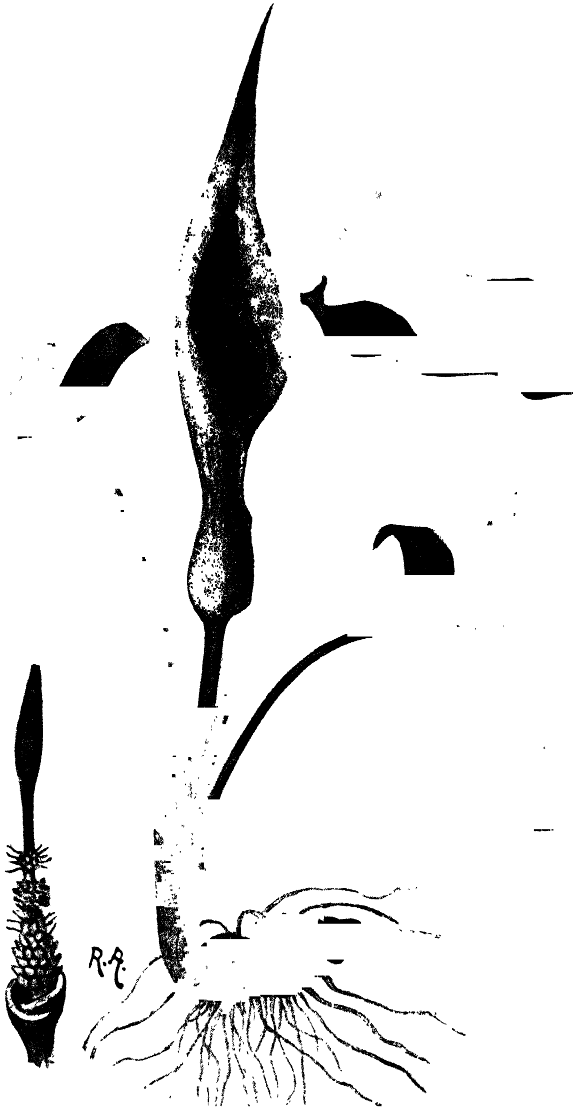


FIG. 828.—*Arum maculatum* ($\frac{1}{2}$ nat. size). Inflorescence and fruits ($\frac{2}{3}$ nat. size). *POISONOUS.*

many seeds. *Luzula*, with flat leaves and three-seeded fruits, one of the earliest spring-flowering plants.

Family 2. **Liliaceae.**—Typical flower, with coloured, conspicuous perianth. Entomophilous. Ovary superior. The fruits are septicidal or loculicidal capsules, or berries. Seeds numerous. Endosperm horny or fleshy.

The majority of the Liliaceae are perennial herbs with bulbs, tubers, or rhizomes. They mainly inhabit the warm temperate regions.

Sub-family 1. **Melanthoideae.**—Capsules septicidal. *Colchicum autumnale*, the Autumn Crocus (Fig. 830), is a perennial herb growing in meadows. If a plant is examined in autumn at the time of flowering, the corm, to the base of which is attached the lateral shoot bearing the flowers, will be seen to be enclosed in a brown envelope. The lateral flowering shoot bears at its base three sheathing leaves not separated by elongated internodes. In the axil of the third of these is a bud which will form the flowering shoot of the next season. In spring the reserve-materials from the corm are absorbed and the old corm is pushed aside by the swollen internode which in its turn enlarges to form a new corm. The three foliage-leaves expand their long, channelled, dark green laminae above the soil; their sheathing portions closely surround the axis. The latter bears the fruits, which contain numerous, spherical, black seeds; these are liberated by the dehiscence of the capsule at the sutures (Fig. 830 *f*). *Veratrum album* is a conspicuous herb with a rosette of large, elliptical, longitudinally-folded leaves. The growth of the main axis is terminated by an inflorescence, which is a panicle more than a metre in height; the leaves borne on it have long sheaths and diminish in size from below upwards. The greenish-white flowers are polygamous. *Schoenocaulon* (*Sabadilla*) *officinale*, a bulbous plant of the Andes with grass-like leaves, has also septicidal capsules. *Bowiea*, twining plant, South Africa. *Gloriosa* and *Littonia*, both with tendril-like leaf-tips and conspicuous flowers.

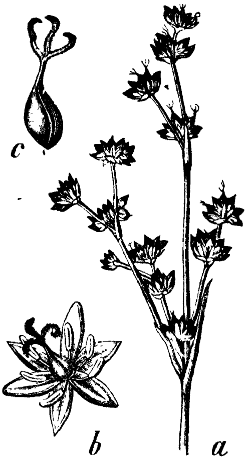


FIG. 829.—*Juncus lamprocarpus*. *a*, Part of an inflorescence; single flower (*b*) and gynaeceum (*c*) magnified. (After A. F. W. SCHIMPER.)

Sub-family 2. **Lilioideae.**—Capsule loculicidal. Includes such popular flowers as *Tulipa* (Fig. 197), *Hyacinthus*, *Lilium* (Fig. 200), *Muscari*, and *Scilla*, and vegetables as *Allium*, together with *Urginea* (Fig. 831), which occurs in the Mediterranean region, *Galtonia*, South Africa. *Ornithogalum umbellatum* (Fig. 832) will serve as an example of this group. In autumn the plant consists of a bulb, each of the fleshy scales of which has a scar at the upper end. In the axil of the innermost scale beside the stalk of the spent inflorescence is a young bud bearing a number of leaves. Each of these leaves is provided with an embryonic lamina, while the continuation of the shoot is the embryonic inflorescence. In spring the leaves grow into long linear structures, and, together with the inflorescence, appear above ground. The inflorescence is sparingly branched; the white flowers have a trilocular ovary bearing a common style. The upper

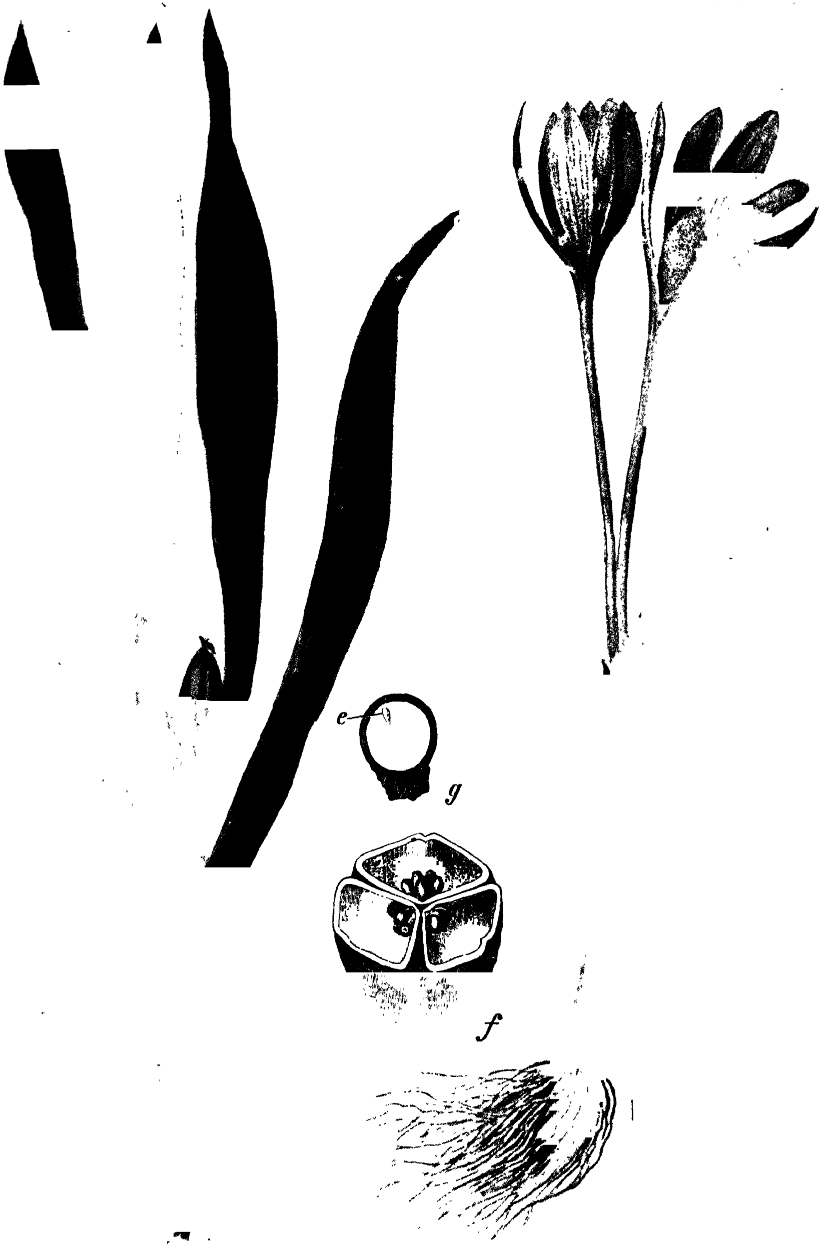


FIG. 830.—*Colchicum autumnale* (½ nat. size). *f*, Fruit in transverse section ; *g*, seed with embryo (*e*) (enlarged). *POISONOUS.*

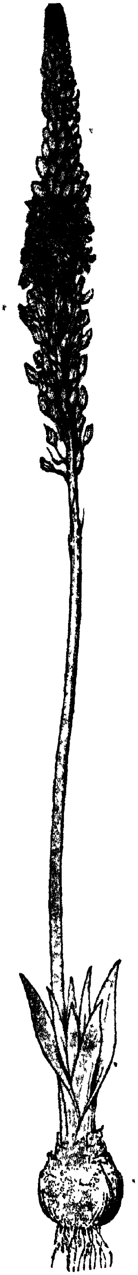


Fig. 831 — *Urginea maritima* (about $\frac{1}{10}$ nat. size) (After Berg [illegible]

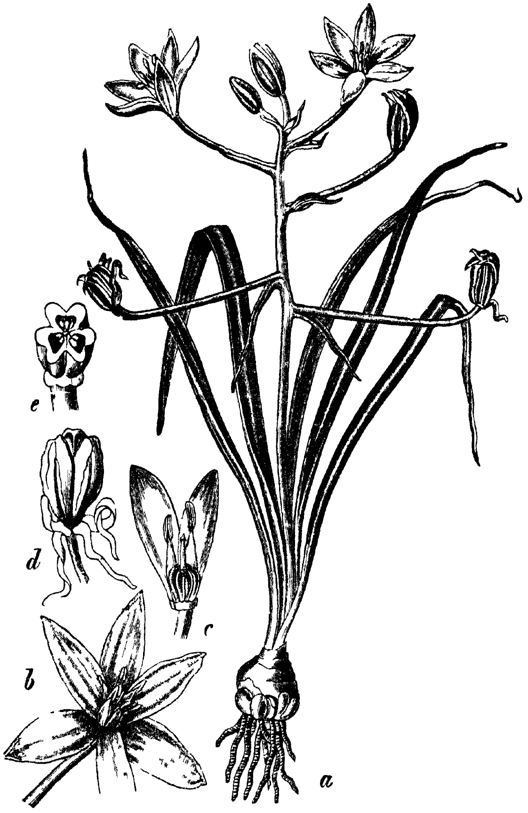


Fig 832 — *Ornithogalum umbellatum* *a* Entire plant (reduced), *b*, flower (nat size); *c*, flower, part of perigone and androecium removed, *d*, fruit, *e*, fruit in transverse section

parts of the leaves wither, while the basal portions become swollen and fleshy, and stored with reserve-materials; the scar at the upper part of each scale marks the place of separation of the leaf-blade. The annual course of development is essentially similar in other bulbous plants. The vegetative period is restricted to a few months, while during the cold or, in the numerous bulbous plants of warm-temperate climates, the dry seasons, the bulb is protected by its subterranean situation. *Aloë*, a genus of African plants containing many species (Figs. 833, 834), has succulent leaves with spiny margins.

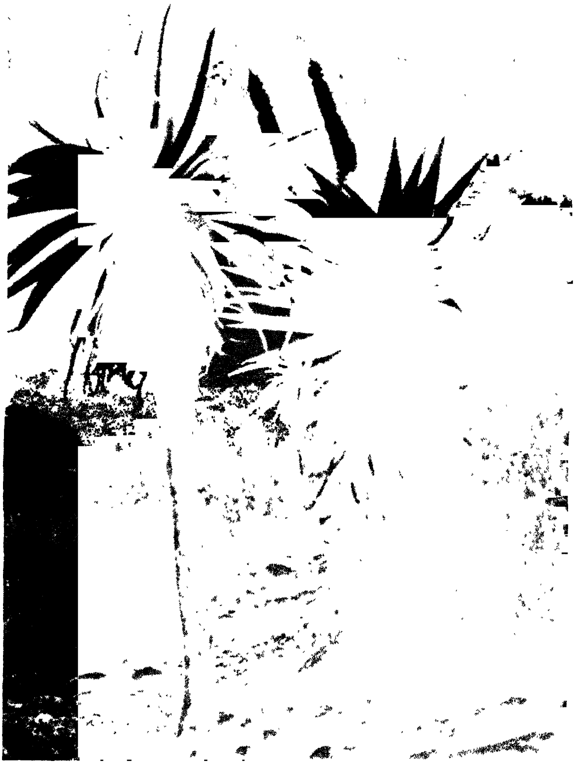


FIG. 833.—*Aloë speciosa* and *Aloë ferox*. The latter with branched inflorescences. (After MARLOTH.)

Sub-family 3. **Asparagoideae.**—Fruit, a berry. *Dracaena* (Fig. 835), an arborescent form which attains a great age and a characteristic appearance, together with the similar genera, *Cordyline* and *Yucca*, and *Smilax* (Sarsaparilla), a shrubby plant of warmer countries, climbing by the help of tendril-like emergences at the base of the petioles, have berries. Other examples are *Asparagus* with bunches of phylloclades in place of leaves, *Ruscus*, with broader leaf-like phylloclades, and *Myrsiphyllum*. *Convallaria* (Fig. 121), *Maianthemum*, *Polygonatum* (Fig. 139), and *Paris quadrifolia* (Fig 836), the latter bears whorls of four leaves, sometimes 3 6 leaves (60) All these plants have creeping rhizomes bearing scale leaves, either the apex of this rhizome grows annually into the erect shoot bearing the foliage leaves and inflorescences, while the growth of the rhizome is continued by a lateral branch (*Polygonatum*), or the rhizome continues its subterranean growth, the leafy shoots being developed from axillary buds (*Paris*)

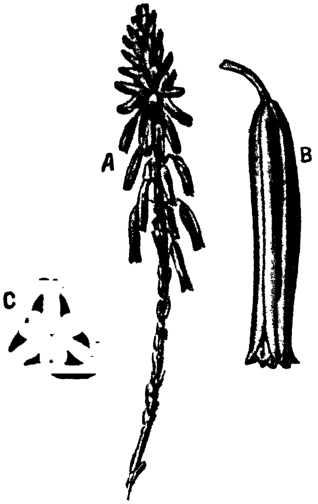


Fig 834 —*Aloe succotrina.* *A*, Inflorescence *B*, Flower *C*, Ovary in cross section

POISONOUS —Numerous Liliaceae are more or less poisonous, *e g* Lily of the Valley, Tulip, *Fritillaria*, *Colchicum*, *Veratrum*, *Paris*

OFFICIAL —*Colchicum autumnale*, COLCHICI CORMUS and SEMINA *Aloë chinensis A Perryi*, and *A. ferox* yield ALOE *Urginea Scilla* yields SCILLA *Urginea indica* yields URGINEA

Family 3 **Amaryllidaceae** (60a) —Distinguished from Liliaceae by the inferior ovary *Leucojum* (Fig 837), the Snowdrop (*Galanthus*), and *Narcissus* resemble the bulbous Liliaceae in habit The majority of the genera belong to the tropics or sub tropics, *e g Haemanthus*, *Clivia*, *Crinum*, species of which are often grown in greenhouses. *Agave*,

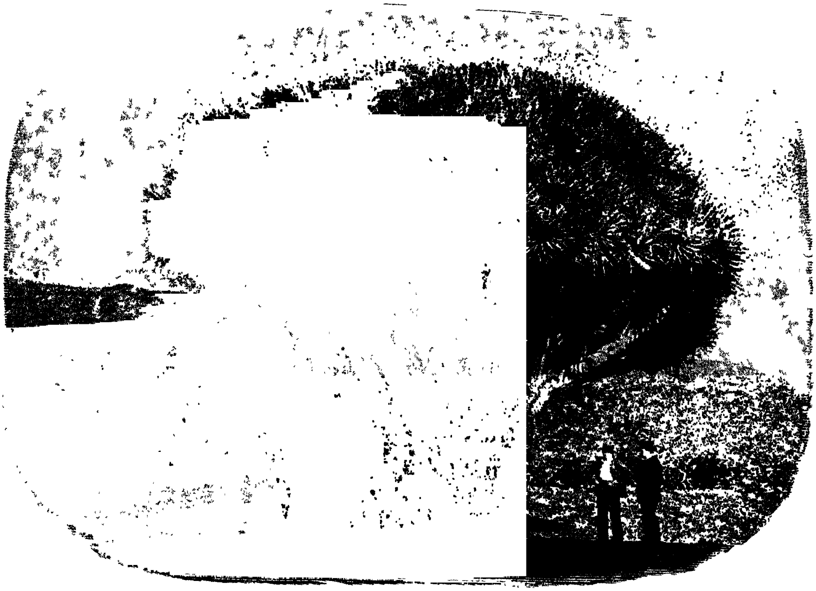


Fig 835 —*Dracaena draco* The Dragon Tree of Laguna in the Canary Islands (After CHUN)

large plants with succulent leaves from the warmer regions of America, provide

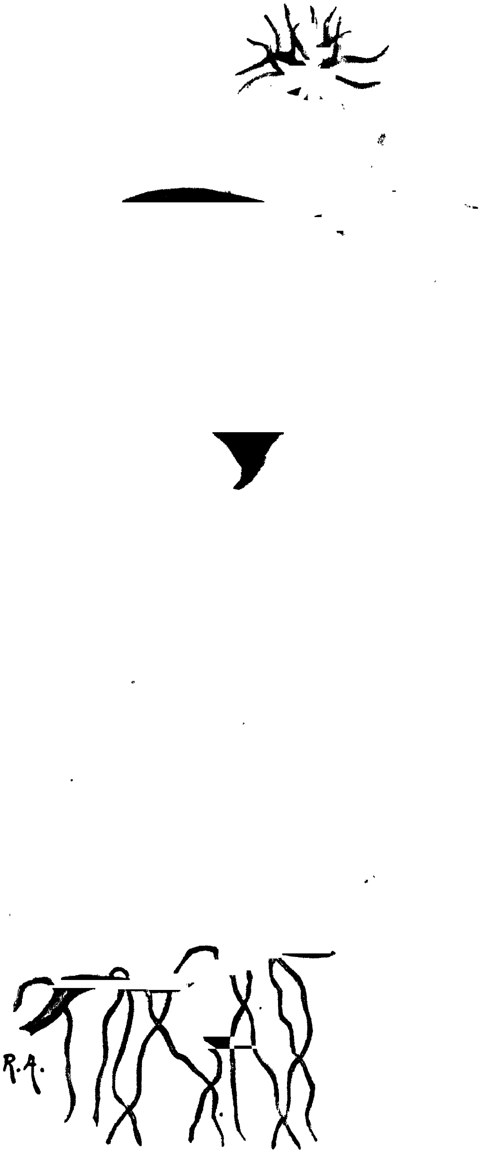


FIG. 836.—*Paris quadrifolia* (½ nat. size). POISONOUS.

fibres. *Agave Sisalana* from Yucatan, one of the most important fibre-yielding plants. *A. salmiana* provides the national drink of Mexico (pulque), obtained by fermenting the sap that flows on cutting off the inflorescence. Species of *Agave* are acclimatised in the Mediterranean region.

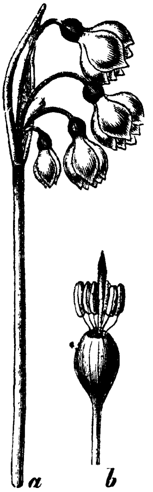


FIG. 837.—*Leucojum aestivum.* *a*, Inflorescence (reduced); *b*, gynaeceum and androecium (nat. size). (After SCHIMPER.)

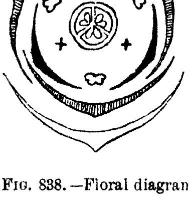


FIG. 838.—Floral diagram of the Iridaceae (*Iris*).

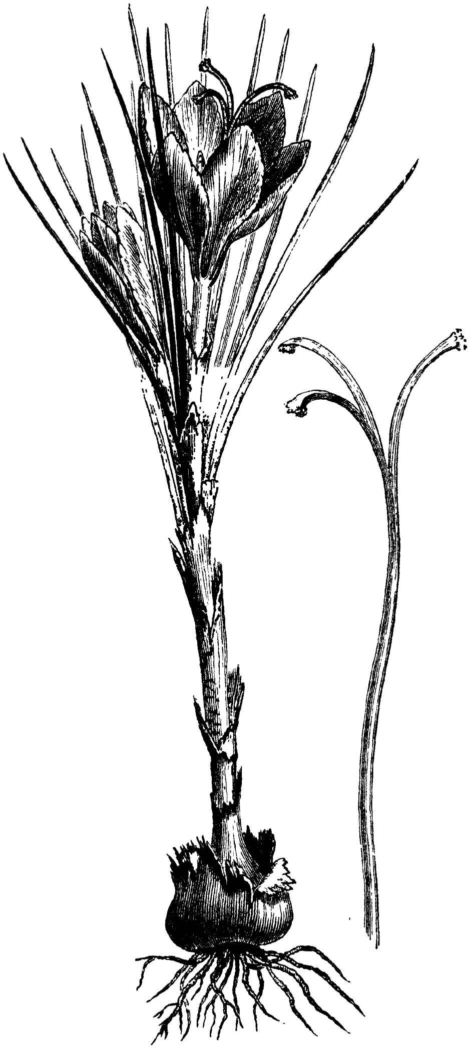


FIG. 839.—*Crocus sativus.* Style with tripartite stigma. (After BAILLON.)

Family 4. **Iridaceae.**—Distinguished from Liliaceae by their inferior ovary and by the suppression of the inner whorl of the androecium (Fig. 838). Cf. the atavistic form *Iris pallida*, Lmk.

forma *abavia* Heinr (p. 559, Fig 550). The two whorls of the perianth are not always similar. Anthers extrorse. The leaves of the Iridaceae are always sessile; the underground portion is a tuberous or elongated rhizome, less commonly a bulb. Capsule loculicidal. This family is mainly represented in the Cape and the warmer parts of America.

Crocus sativus, Saffron (Fig. 839), is a plant which has long been cultivated in the East; it has a tuberous rhizome and narrow, grass-like leaves. The flowers are sterile unless pollinated with pollen of the wild form. The large stigmas furnish Saffron. Other species are cultivated as ornamental plants. *Iris*, leaves overlapping in two ranks. The leaf-sheath surrounds the thick fleshy rhizome, while the sword-shaped blade stands erect and has its two lateral surfaces alike (Fig. 840). Outer perianth segments bent downwards, inner erect. The three anthers are roofed over by the three leaf-like styles, which have a small, triangular stigmatic lobe on their outer sides. In *Gladiolus* the flowers are dorsiventral, and the dissimilarity of the perianth leaves is more marked.

Family 5. **Bromeliaceae.**—Mostly epiphytes (*e.g.* *Tillandsia*); flowers hermaphrodite. Limited to tropical and sub-tropical parts of America. The leaves are in rosettes and are typically xeromorphic; in the forms which grow in the soil they are spiny; such plants have frequently ornithophilous flowers. *Ananassa sativa* is cultivated; its inflorescence forms the Pineapple.

Order 4. Enantioblastae

Characterised by the atropous ovules; the embryo is at the summit of the endosperm at the opposite end from the hilum.

Family. **Commelinaceae.** Tropical and sub-tropical. Perianth developed as calyx and corolla. *Commelina*, *Tradescantia*. The hairs of the stamens afford well-known objects for the study of movements of protoplasm and nuclear divisions. *Rhoeo discolor*; Mexico, in cultivation.

(*b*) *Flowers more or less reduced*

Order 5. Glumiflorae

This order consists entirely of annual or perennial plants of grass-like habit. It is distributed over the whole surface of the earth. A woody stem only appears in the genus *Bambusa*. The association in more or less complex inflorescences of numerous flowers, which lack a proper perianth but are enclosed by scaly bracts (glumes), is a common character of the order. The perianth is either completely wanting or reduced to a series of scales or bristles. The inner whorl of stamens is also usually wanting. The superior ovary is always unilocular and contains only one ovule; it is formed of three (Cyperaceae), two (some Carices), or of a single carpel (Gramineae). The large size and feathery and papillose form of the stigmas stand in relation to the wind-pollination. Fruits indehiscent.

Family 1. **Cyperaceae.**—The Sedges are characterised by their triangular stems, which are usually neither swollen at the nodes nor hollow, and by their

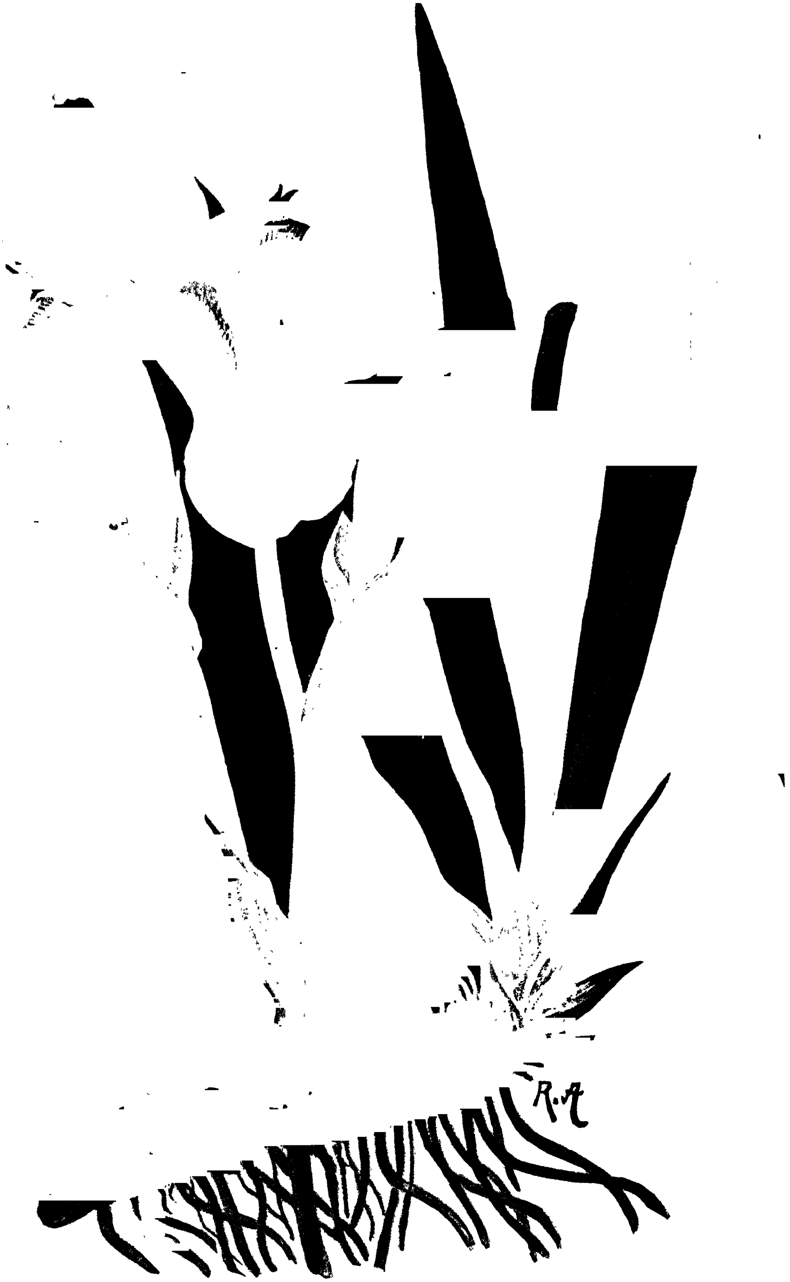


FIG. 840.—*Iris germanica* (½ nat. size).

closed leaf-sheaths. The flowers are either unisexual and then usually monoecious (*Carex*) or are hermaphrodite as in the majority of the genera; ovary formed of two or three carpels with an erect, basal, anatropous ovule. Pericarp not coherent with the seed-coat; embryo small, surrounded by the endosperm.

The genera *Cyperus*, *Scirpus*, and *Eriophorum* have hermaphrodite flowers. Fig. 841 represents a plant of *Scirpus setaceus*, which is an annual, in flower. Leaves rigid, channelled above. Fertile shoots with the uppermost internode elongated. Spikes 1-3, terminal; enclosed by imbricating bracts and displaced to one side by the subtending bract, the line of which continues that of the stem. Only the large lowermost bracts are sterile, the others have each a naked, hermaphrodite flower in their axils. The Cotton-grass (*Eriophorum angustifolium*), which when flowering is inconspicuous, bears at the summit of its fertile shoots 3-7 long-stalked erect spikelets with numerous imbricate bracts. Around the base of each flower are numerous hairs, which are concealed by the projecting stamens and style. When the plant is in fruit the hairs, which have become about 3 cm. long, project freely from between the bracts and constitute a valuable means of dispersal for the fruits. The white colour of the hairs makes

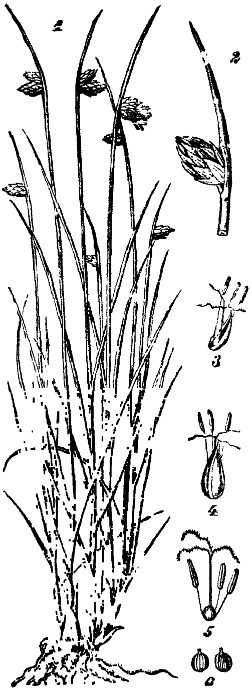


FIG. 841.—*Scirpus setaceus*. *1*, Plant in flower; *2*, upper portion of a flowering shoot; *3*, single flower; *4*, the same from behind; *5*, the same without the bract; *6*, fruit. (*1*, nat. size, the others × 2-6. After HOFFMANN.)

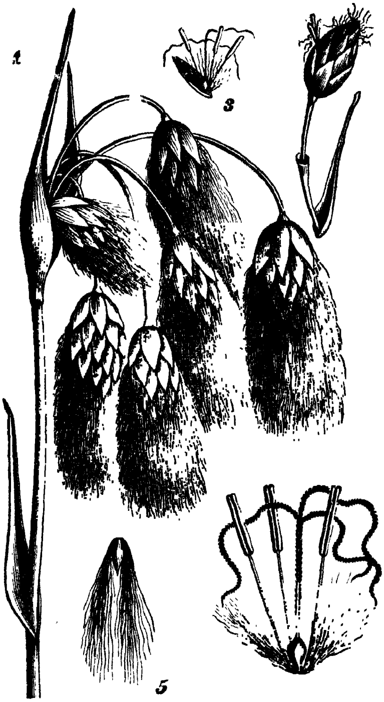


FIG. 842.—*Eriophorum angustifolium*. *1*, Inflorescence; *2*, a single spikelet; *3*, single flower; *4*, flower with bract removed; *5*, fruit. (*1*, about nat. size, the others × 3-5. After HOFFMANN.)

the now pendulous spikelets of the Cotton-grass a conspicuous feature of peat-moor vegetation (Fig. 842). *Cyperus papyrus*, in Egypt and Sicily, provided from its stems, which are as thick as the thigh, the "paper" of the ancient Papyri.

The genus *Carex* is for the most part monoecious, and its flowers are naked and unisexual. Male spikes simple; in the axil of each bract is a male flower formed of three stamens (Fig. 843 *A*). The female spikes bear in the axil of each bract a secondary shoot; the axis of this is included in the tubular subtending bract (utriculus) together with the pistil (formed of two or three carpels), which is borne in the axil of the bract (Fig. 843 *B-E*).

Family 2. **Gramineae** (61).—The stems of the true Grasses are cylindrical, and have hollow internodes (exceptions Maize and Sugar-cane); the nodes are swollen; the leaves are two-ranked and their sheath is usually split and thickened at the node. At the junction of the sheath and leaf-blade a membranous structure (the ligule) projects (cf. Fig. 134). The flowers of the Gramineae are grouped in spicate, racemose, or paniculate inflorescences, which are always composed of partial inflorescences, the spikelets.

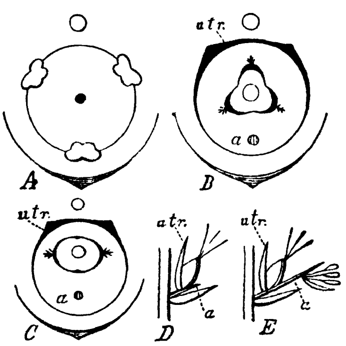


FIG. 843.—*A*, Floral diagram of a male flower of *Carex*; *B*, of a female flower with three stigmas; *C*, of a female flower with two stigmas. *D*, Diagram of female flower of *Carex*. *E*, Diagram of the hermaphrodite spikelet of *Elyna*; *a*, secondary axis; *utr*, utriculus or bract of the secondary axis. (After EICHLER.)

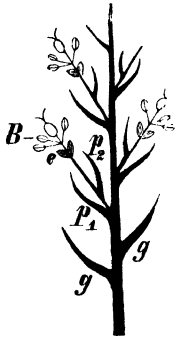


FIG. 844. — Diagrammatic representation of a Grass spikelet. *g*, The glumes; p_1 and p_2, the inferior and superior palea; *e*, lodicules; *B*, flower. The axial parts are represented as elongated.

Usually each SPIKELET bears several flowers. At the base of the spikelet there are usually (Fig. 844) a pair of sterile bracts (GLUMAE); sometimes there is only one or 3-4 glumes. Continuing the two-ranked arrangement of the glumes come the fertile subtending bracts (PALEA INFERIOR), in the axil of each of which stands a flower. The subtending bracts are often awned, *i.e.* they bear, terminally or springing from the dorsal surface, a stiff bristle with backwardly directed hairs (the AWN). The bracteole of each flower is represented by another scale-like bract, the PALEA SUPERIOR. Above this come two small scales, the LODICULAE, the distension of which assists in opening the flower (Fig. 561). Lastly, the axis bears the androecium consisting of a whorl of three stamens, and the ovary composed of one carpel and bearing two feathery papillose stigmas. The ovary contains an anatropous, or slightly campylotropous ovule.

The flowers do not always show such extreme reduction; thus the flower of Rice (Fig. 850) has a complete androecium; that of the Bambuseae is similar and also has three lodicules, and in *Streptochaeta* there is a normal monocotyledonous type of flower with all five whorls of members present and three carpels indicated in the development of the ovary. The lodicules can on this evidence be regarded as corresponding to the inner whorl of the perianth. Possibly the superior palea represents two coherent leaves of the outer whorl. In the gynaeceum there remains, as a rule, only a double leaf formed of the two lateral carpels of the three originally present. According to this view, which we owe to von Goebel, the diagram in Fig. 845 is arrived at.

On the wind-pollination of Grasses cf. p. 563. The fruit of the Grasses is termed a caryopsis; in it the pericarp and seed-coat are intimately united. The embryo lies in contact with the endosperm by means of its cotyledon; this forms the scutellum, and in germination serves as an absorbent organ by means of which the reserve-materials in the endosperm are taken up by the seedling (Fig. 847).

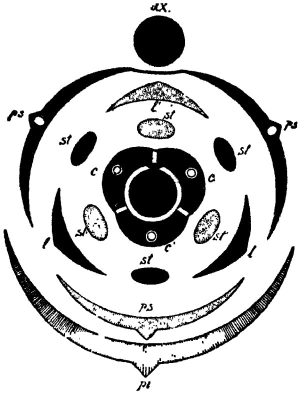


Fig. 845.—Diagram of the Grass flower. The missing parts are dotted; *ax*, end of the axis of the spikelet; *pi*, palea inferior; *ps*, palea superior (outer perigone); *l* lodiculae (inner perigone); *st*, outer, *st'*, inner whorl of stamens; *c*, lateral carpels; *c'*, dorsal carpel. (After Schuster.)

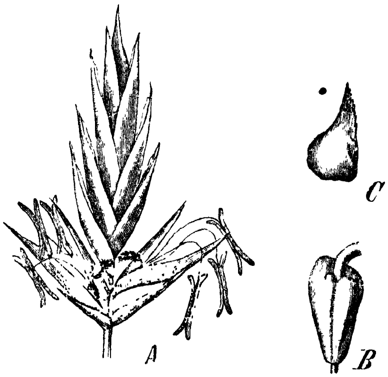


Fig. 846.—*Festuca elatior*. *A*, Spikelet (compare Fig. 844), with two open flowers below which the two sterile glumes are seen (×3). *B*, Ovary seen from the side with the stalk of one of the removed stigmas (×12). *C*, A single lodicule (×12). (After H. Schenck.)

The most important economic plants belonging to this order are the Cereals (Fig. 848). Wheat, *Triticum* (Fig. 848 *B*, *D*). Spikelets single, with two or more flowers; glumes broadly ovate (Fig. 849 *B*). Koernicke distinguishes as species of Wheat — (1) *Tr. vulgare*, with a number of sub-species; (2) *Tr. polonicum*; (3) *Tr. monococcum*. Rye, *Secale cereale* (Figs. 848 *A*, 849 *A*); spikelets single, two-flowered; glumes acute. Barley, *Hordeum vulgare* (Fig. 848 *C*); spikelets one-flowered, in groups of three; in the sub-species *H. hexastichum* and *H. tetrastichum* all the rows of spikelets are fertile, in *H. distichum* only the middle row. Oat, *Avena sativa*. Maize, *Zea mais*. The above are all cultivated in temperate climates, the Maize largely in America, the others also in Western Asia and the south-east of Europe. In the wild state only *Triticum monococcum*, var. *aegilopodioides* (from which *Tr. monococcum* is derived), *Triticum dicoccoides* as the original form of Wheat, *Secale montanum*, and *Hordeum spontaneum* (allied to *H. distichum*) are known. In these wild forms the spikelets fall from the rachis at maturity, a character that would be unsuitable in cultivated forms.

The most important tropical food-plant of the order is Rice, *Oryza sativa* (Fig. 850), which is largely cultivated to the limits of the warmer temperate regions, and, when sufficient moisture is available, yields an enormous harvest (Fig. 851). In Africa several varieties of Millet, *Andropogon Sorghum*, are cultivated, and it forms the most important cereal for that continent. *Panicum miliaceum* and *P. italicum*, of Asiatic origin, are still cultivated, though to a diminished extent, in the Mediterranean region. The Sugar-cane, *Saccharum officinarum*, is another important food-plant; it is a perennial, growing more than six feet high, and occurs in tropical Asia. The Sugar-cane is cultivated in all tropical countries, and cane-sugar is obtained from the sap expressed from the solid stem.

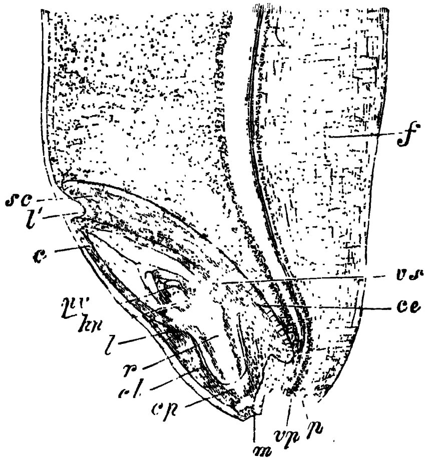


Fig. 847.—Part of median longitudinal section of a grain of Wheat, showing embryo and scutellum (*sc*); *vs*, vascular bundle of scutellum; *ce*, its columnar epithelium; *l'*, its ligule; *c*, sheathing part of the cotyledon; *pv*, vegetative cone of stem; *hp*, hypocotyl; *l*, epiblast; *r*, radicle; *cl*, root-sheath; *m*, micropyle; *p*, funiculus; *vp*, its vascular bundle; *f*, lateral wall of groove; *cp*, pericarp. (× 14.) (After Strasburger.)

Among the most important of our meadow-grasses may be mentioned *Agrostis alba*, *Alopecurus pratensis*, *Anthoxanthum odoratum*, *Arrhenatherum elatius*, *Avena flavescens*, *A. pubescens*, *Briza media*, *Dactylis glomerata*, *Holcus lanatus*, *Lolium perenne*, *Phleum pratense*, *Poa pratensis*, and species of *Aira*, *Bromus*, *Calamagrostis*, *Festuca*, *Melica*, etc. The tropical species of *Bambusa*, which grow to the height of trees, are utilised in many ways; from the stems are constructed houses, walls, flooring, ladders, bridges, cordage, water-vessels, cooking utensils, water-pipes, etc., and the plant is indispensable in the countries in which it occurs.

Poisonous.—*Lolium temulentum* (Fig. 852) has its fruits, as a rule, infested with fungal hyphae. These fruits owing to the alkaloids they contain are poisonous, but fruits free from fungus are harmless (^{C2}); the plant is an annual, and can be distinguished by the absence of sterile shoots from the common *Lolium perenne* and *L. multiflorum*. It is the only poisonous grass.

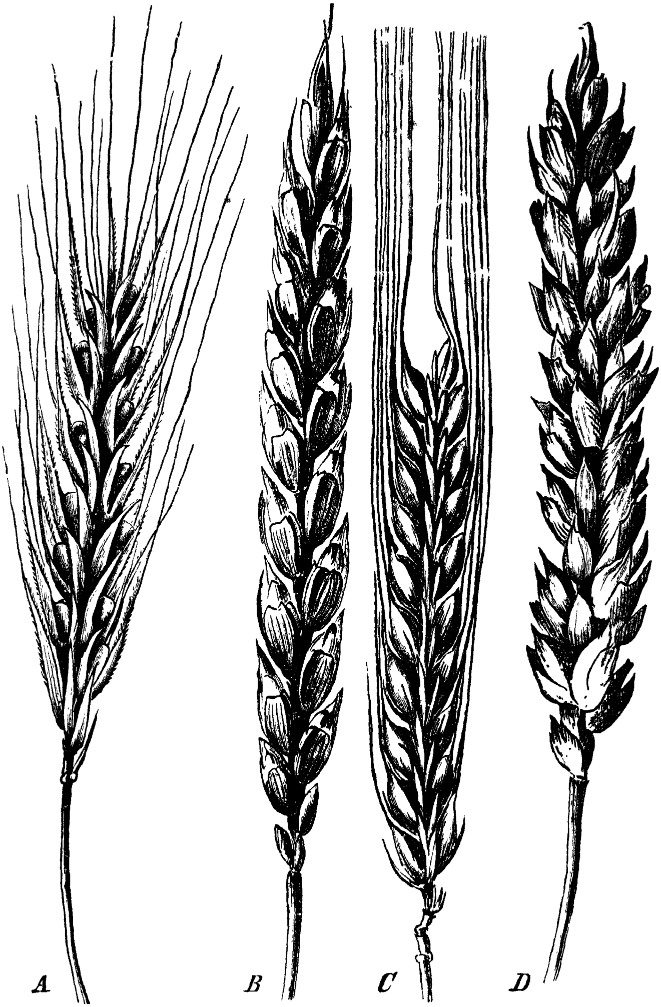


FIG. 848.—Cereals. *A*, Rye, *Secale cereale*. *B*, Spelt, *Triticum Spelta*. *C*, Two-ranked barley, *Hordeum vulgare, distichum*. *D*, Wheat, *Triticum vulgare*.

OFFICIAL.—AMYLUM (starch) is obtained from *Triticum sativum, Oryza sativa, Zea mais*, etc.; *Agropyron repens* yields AGROPYRUM. *Saccharum officinarum* provides SACCHARUM PURIFICATUM.

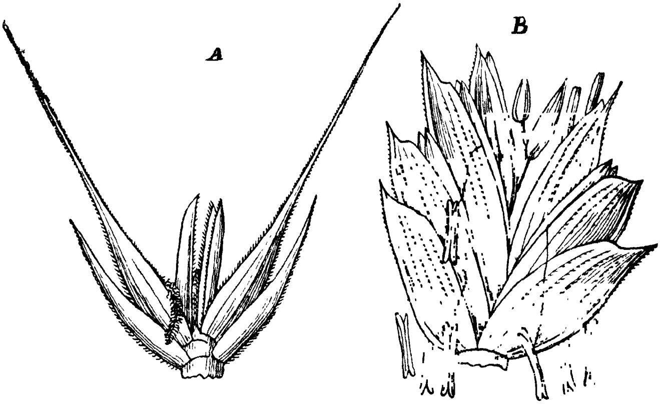


FIG. 849.—*A*, Spikelet of Rye; two-flowered. *B*, Spikelet of Wheat with a number of flowers.

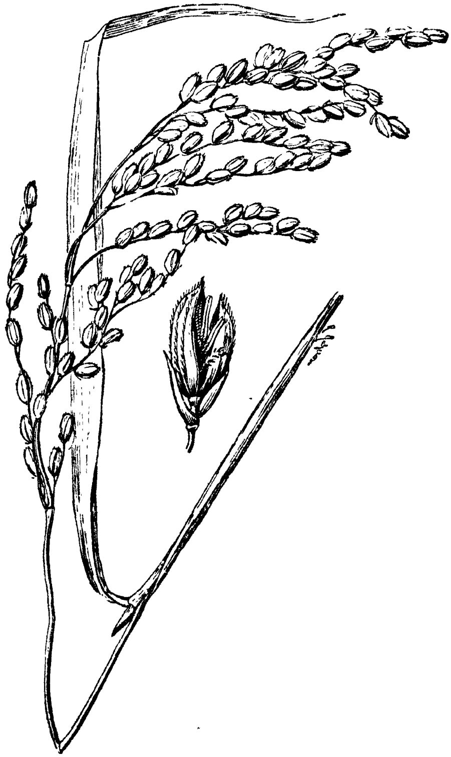


FIG. 850.—*Oryza sativa*. Panicle (½ nat. size), and a single spikelet (enlarged).

(c) *Flowers zygomorphic*

Order 6. Scitamineae

Tropical plants, sometimes of large size, in a few cases arborescent. Flowers dorsiventral or asymmetrical. Perianth differentiated into calyx and corolla. Androecium greatly reduced; some of the stamens represented by staminodes, and resembling the segments of the corolla. Ovary inferior, trilocular. Seeds with perisperm.

FIG. 851.—Terraced land in Ceylon for the cultivation of Rice. The water required for the young plants flows from terrace to terrace through gaps in the boundary walls. In the foreground Bananas, and to the right a Coffee plantation. In the centre Areca palms. (From a photograph.)

Family 1. **Musaceae.**—The Banana, *Musa sapientum* (Fig. 853), is one of the most important plants of all tropical countries. The apparent, erect stem is formed of the closely overlapping, sheathing bases of the large leaves. Inflorescence, terminal, pendulous, bearing the crowded and mainly parthenocarpic (63), berry-like fruits. *M. textilis* yields Manila Hemp. *Ravenala* has a woody stem. *Strelitzia reginae* (Fig. 564) from the Cape is cultivated on account of the beauty of its ornithophilous flowers.

Family 2. **Zingiberaceae.**—Flowers in spikes, which in some cases resemble capitula. Flower dorsiventral. Calyx inconspicuous, tubular. Corolla with three lobes. The outer whorl of the androecium is wanting or represented by two lateral staminodes (Fig. 854, sst_1, sst_2). Only the posterior stamen of the inner whorl (*st*) is fertile; the two others are joined to form the brightly-coloured petaloid labellum (*l*). The style lies in the tubular groove between the thecae of the stamen. Fruit, a capsule. Most plants of the family belong to tropical Asia.

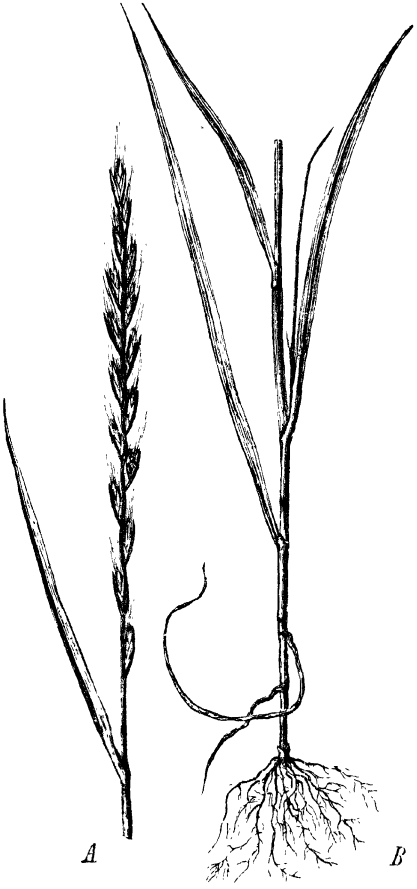


FIG. 852.—*Lolium temulentum*. POISONOUS. (After H. SCHENCK.)

Zingiber officinale, the Ginger, is an ancient cultivated plant of Southern Asia, now cultivated throughout the tropics (Fig. 855). The flattened branched rhizome is in contact with the soil by its narrow side. Leaves, two-ranked; main shoot continued by the growth of axillary buds of the lower surface. The leafy shoots, in spite of their length, are composed of the sheaths of the large, simple, entire leaves, the axis remaining extremely short. Only the flowering shoots are solid; they remain shorter and bear scale-leaves with large sheaths but no laminae. Bracts large and, especially at their margins, brightly coloured. Flowers, bright yellow, with a conspicuous, violet, and spotted labellum. *Elettaria Cardamomum* and *Curcuma* have the stalks bearing their inflorescences similarly provided with scale-leaves. *Alpinia* and *Hedychium*, the latter of which is often cultivated, have on the other hand normal leafy shoots bearing the terminal inflorescence.

OFFICIAL.—*Zingiber officinale*, rhizome yields ZINGIBER. *Elettaria Cardamomum* yields CARDAMOMI SEMINA.

Family 3. **Cannaceae.**—Large-leaved herbs; often in cultivation. Flowers asymmetrical (Fig. 551 *C*). Only one half stamen fertile (*i.e.* anther with only one theca), the other half being petaloid.

FIG. 853.—*Musa sapientum* along with *Manihot utilissima*. Ceylon. From a photograph.

Family 4. **Marantaceae.**—Large-leaved herbs. Leaves with pulvinus at junction of stalk and lamina. Stamen as in preceding order. ARROWROOT is obtained from *Maranta arundinacea*.

Order 7. Gynandrae

Family **Orchidaceae.**—Perennial, herbaceous plants growing as epiphytes or in the ground, with hermaphrodite, zygomorphic flowers. Perianth petaloid, the posterior segment of the inner whorl developed as a lip or labellum, which frequently bears a spur.

The "labellum" of the Scitamineae being formed of two staminodes is entirely different morphologically.

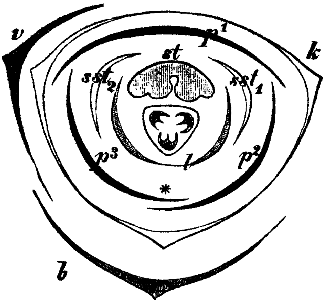


FIG. 854.—Floral diagram of Zingiberaceae (after EICHLER). *b*, Bract; *v*, bracteole; *k*, calyx; p^{1-3}, segments of corolla; sst_1, sst_2, staminodes of the outer whorl of the androecium; *, the suppressed stamen of this whorl; *st*, the single fertile stamen; *l*, petaloid staminodes of the inner whorl of the androecium forming what is known as the labellum.

FIG. 855.—*Zingiber officinale.* (½ nat. size. After BERG and SCHMIDT.)

Androecium formed of the three anterior stamens only; the middle stamen, belonging to the outer whorl, is fertile; the other two are represented by staminodes. Gynaeceum formed of three carpels, syncarpous; ovary inferior, unilocular. Fruit, a capsule. Seeds extremely numerous, borne on parietal placentas (Figs. 856, 859). The fertile stamen is adherent to the style and forms with it the COLUMN or GYNOSTEMIUM; this projects more or less in the centre of the flower. The labellum, which serves as an alighting place for visiting insects, becomes anterior, either by the torsion of the whole flower through 180° or by the flower being bent backwards.

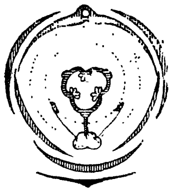


FIG. 856.—Orchidaceae. Floral diagram (*Orchis*). (Modified after NOLL.)

The Orchidaceae attain their highest development in the tropics where they form an important part of the epiphytic vegetation. Large water-storage tubers at the bases of the leaves, or succulence of the whole plant, is found in the epiphytic forms. *Orchis*, *Ophrys*, *Gymnadenia*, *Platanthera* with tubers; *Epipactis*, *Cephalanthera*, *Listera* with branched rhizomes; *Neottia*, the Bird's-nest Orchid, *Epipogon*, *Coralliorrhiza*, *Limodorum* almost destitute of chlorophyll. They live saprophytically or more correctly as parasites at the expense of their mycorrhiza ([64]). *Cypripedium*, Ladies' Slipper, with two lateral fertile stamens of the inner whorl.

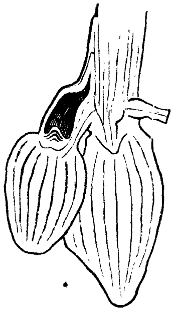


FIG. 857.—*Orchis militaris*. Longitudinal section passing through the old and new tubers. (After LUERSSEN.)

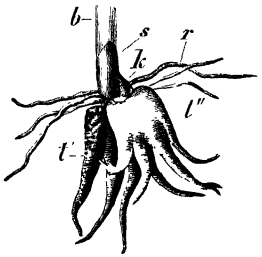


FIG. 858.—Root-system of *Orchis latifolia*. *b*, Base of stem: *s*, scale-leaf; *t'*, old, *t''*, young tubers; *k*, bud; *r*, roots. (After H. SCHENCK.)

Orchis militaris, which is represented in Figs. 859, 861, will serve as an example for more detailed consideration. At the period of flowering a pair of fleshy tubers will be found at the base of the plant, both of which are covered with root hairs. The large or brown tuber of more spongy texture continues above into the stem which terminates in the pyramidal inflorescence; this stem is surrounded at the base by a pair of scale-leaves and the sheaths of the 2-4 elongated, elliptical foliage-leaves. The smaller tuber is of firmer consistence and of a white colour; it bears, as is shown in the longitudinal section (Fig. 857), a bud on its summit which already shows a pair of scale-leaves. This tuber has arisen as an axillary bud in relation to one of the first scale-leaves of the plant, and with its tuberous, swollen, first root has broken through the subtending scale-leaf (Fig. 861). It is destined to replace the parent-plant in the succeeding season.

In considering the flower, the spiral torsion of the ovary, which brings the labellum into the anterior position, must first be recognised. The labellum is tripartite and the larger middle segment is bifid at its free end. At the base of the labellum a spur is formed by the bulging out of this segment of the perianth ; this serves as the nectary, and the opening leading into it is situated just below the gynostemium (Fig. 859 *A*, *B*). The latter bears on the side that is turned towards the lower lip, and to an insect alighting on this, the large stigmatic surface (*h*) corresponding to two confluent stigmatic lobes. The third stigmatic lobe is transformed into a structure termed the rostellum (*l*, *k*) and stands in relation to the male organ. The single fertile anther consists of two thecae joined together by the connective which appears as the end of the gynostemium. The whole mass of pollen of each of the two pollen-sacs is joined together by an interstitial substance which continues below to form a stalk ; the whole structure, which has a waxy consistence, is called a pollinium, and the stalk goes by the name of the caudicle. The caudicles terminate below in contact with the rostellum which forms tough, adhesive discs. This relation to the rostellum serves to keep the pollinia, which

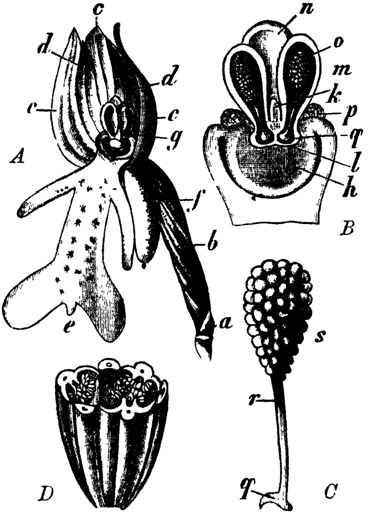


Fig. 859.—*Orchis militaris*. *A*, Flower : *a*, bract ; *b*, ovary ; *c*, the outer, and *d*, the two anterior inner perigone leaves ; *e*, labellum with the spur *f* ; *g*, gynostemium. *B*, Flower after removal of all of the perigone leaves with exception of the upper part of the labellum : *h*, stigma ; *l*, rostellum ; *k*, tooth-like prolongation of the rostellum ; *m*, anther ; *n*, connective ; *o*, pollinium ; *q*, viscid disc ; *p*, staminodium. *C*, A pollinium : *r*, caudicle ; *s*, pollen. *D*, Fruit in transverse section. (After Berg and Schmidt.)

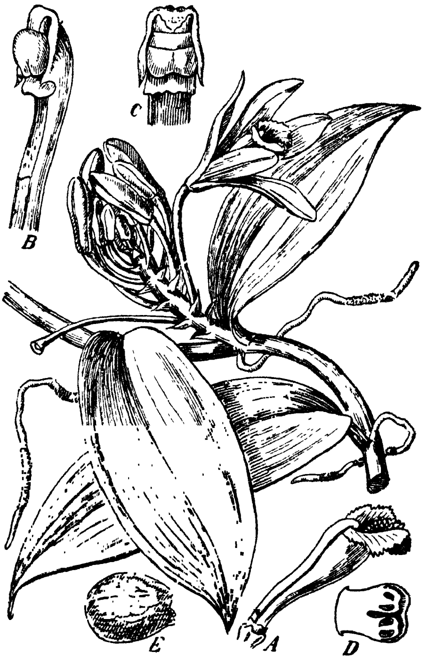


Fig. 860.—*Vanilla planifolia* (reduced. After Berg and Schmidt ; from Engler and Prantl). *A*, Labellum and gynostemium. *B*, Gynostemium from the side. *C*, Summit of the gynostemium from in front. *D*, Anther. *E*, Seed. (Magnified.)

lie free in the pollen-sacs, in position, and the adhesive discs attach the pollinia to any body that comes in contact with them. If an insect alights on the lower lip and attempts to reach the nectar secreted in the spur, its head or tongue must touch the rostellum and the pollinia will become attached to it. As the adhesive discs dry they cause the pollinia to bend forward, so that when the insect visits a second flower they will be brought in contact with the stigmatic surfaces.

All Orchids are similarly adapted to insect visitors, though in many the contrivances are far more complicated; pollination does not take place in the absence of the insects (65). In many cases the adaptations are so specialised to particular insects that no other insect will do instead. The instance of *Vanilla* (Fig. 860) has already been considered. It should be mentioned that in some forms, *e.g. Vanilla*, the pollen remains powdery. Many tropical Orchids are cultivated in greenhouses on account of the beauty of their flowers, *e.g. Cattleya, Laelia, Vanda, Dendrobium, Stanhopea*, etc.

Fossil Angiosperms

The first undoubted Angiosperms appear in the Upper Cretaceous. They are represented by numerous species which, like the recent forms, can be divided into Monocotyledons and Dicotyledons.

The Angiosperms of the Eocene and the Oligocene can be determined with consider-

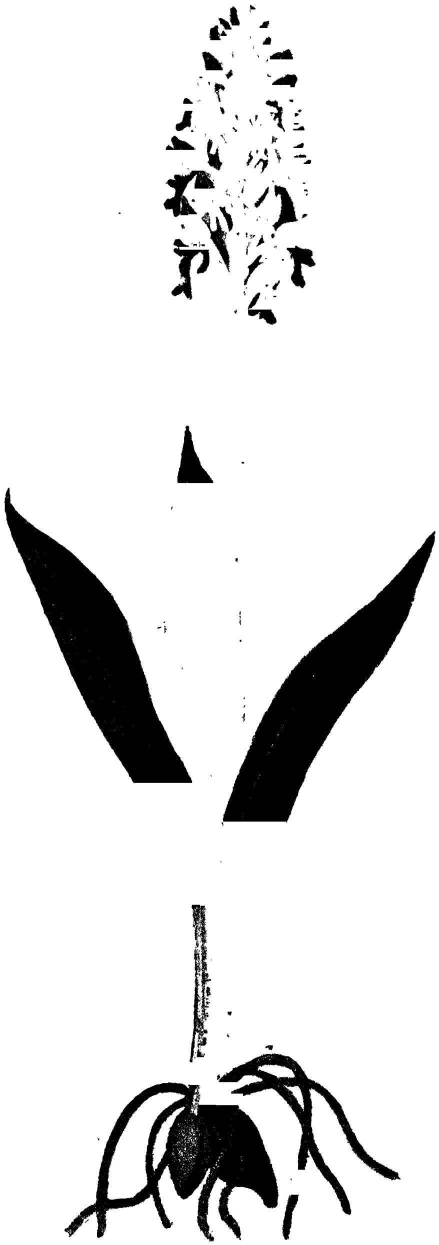


FIG. 861.—*Orchis militaris* (½ nat. size).

able certainty; even in Northern Europe representatives of existing tropical and sub-tropical families occurred, *e.g.* Palmae, *Dracaena*, *Smilax* among Monocotyledons, numerous Cupuliferae (esp. *Quercus*), Lauraceae (*Cinnamomum*, etc.), Leguminosae, etc., among Dicotyledons. From the Miocene onwards the specific forms are in part identical with those now living, and in the Quaternary strata all the remains are of existing species. The general character of the Tertiary flora in Europe was, however, very different from that of the present day. It had the aspect of the flora of a much warmer region and (as in the case of the Gymnosperms) contained forms which now exist only in distant regions.

INDEX OF LITERATURE

INTRODUCTION AND MORPHOLOGY, BY H. FITTING

INTRODUCTION

1. Charles Darwin, On the origin of species by means of natural selection, 1859.

2. H. Fitting, Die Pflanze als lebender Organismus, Jena 1917.

3. C. v. Nägeli, Theorie der Abstammungslehre, 1884, p. 326. F. A. Went, Biol. Zentralbl., vol. 27, 1907, p. 257. K. Goebel, Organographie, 3. Aufl., vol. 1, 1928, p. 13 ff. *Ib.*, Entfaltungsbewegungen d. Pflanzen, 2. Aufl., Jena 1924.

Section I. CYTOLOGY

The Living Cell Contents.

4. A. Meyer, Morphol. u. physiol. Analyse d. Zelle d. Pflanzen u. Tiere, I-II, Jena, 1920-26. G. Tischler, Allgemeine Pflanzenkaryologie, Handb. d. Pflanzenanatomie, I, Berlin, 1921. H. Lundegårdh, Zelle u. Cytoplasma, *ib.*, I, 1921.

5. Literature collected by R. Lieske, Bakterien u. Strahlenpilze, Handb. d. Pflanzenanatomie, VI, Berlin, 1922.

6. A. J. Ewart, Physics and physiology of protoplasmic streaming in plants, Oxford 1903. A. Meyer, Morphol. u. physiol. Analyse d. Zelle, I, p. 631, Jena 1921. H. Fitting, Jahrb. f. wiss. Bot., vol. 64, 1925, p. 281, vol. 67, 1927, p. 427.

7. J. W. Moll, Progress. rei botan., vol. 2, 1908, p. 227. E. Strasburger, Das kleine bot. Praktikum, 10. Aufl. 1923, and Das bot. Praktikum, 7. Aufl. 1923. H. Sieben, Einführung in die bot. Mikrotechnik, 2. Aufl., Jena 1920.

8. E. Zacharias, Progress. rei bot., vol. 3, 1910, p. 67. A. Meyer, cf. under 4. A. Pratje, Biol. Zentralbl., vol. 40, 1920, p. 88. H. Walter, Biochem. Ztschr., vol. 122, 1921, p. 86. A. Kiesel, Ztschr. f. physiol. Chemie, vol. 167, 1927, p. 141.

9. A. Fischer, Fixierung, Färbung und Bau des Protoplasma, 1899, and A. Degen, Bot. Ztg. 1905, I. Abt., p. 202. R. Schaede, Protoplasma, vol. 3, 1927, p. 145.

10. W. Lepeschkin, Kolloidchemie des Protoplasmas, Berlin 1924.

11. P. N. Schürhoff, Plastiden, Handb. d. Pflanzenanatomie, I*, Berlin 1924, p. 14. A. Guilliermond, Ann. scienc. nat. Botanique, 10. Sér., vol. 6, 1924, p. 5.

12. G. Tischler, cited in 4. P. N. Schürhoff, Zytologie d. Blütenpflanzen, Stuttgart 1926.

13. Cf. also K. Bělař, Der Formwechsel der Protistenkerne, Jena 1926.

14. P. N. Schürhoff, cited in 11.

15. Cf. R. Willstätter and A. Stoll, Untersuchungen über Chlorophyll, Berlin 1913. C. v. Wisselingh, Flora, vol. 107, 1915, p. 371. H. Kylin, Ztschr. f. physiol. Chemie, vol. 157, 1926, p. 148 ; vol. 163, 1927, p. 229.

16. E. Goebrig, Beih. Bot. Zentralbl., vol. 35, I., 1918, p. 1.

17. J. Kisser, Sitzungsber. Akad. Wiss. Wien, math.-nat. Kl., I., vol. 131, 1922, p. 105. Fr. Smith, Ann. of bot., vol. 37, 1923, p. 63.

18. J. W. Bailey, Proceed. nat. acad. of science, vol. 5, 1919, p. 283 ; vol. 6, 1920, p. 197. Journ. of gen. physiolog., vol. 2, 1920, p. 519. B. Goldstein, Bull. Torrey bot. Club, vol. 52, 1925, p. 197.

19. R. A. Harper, Jahrb. f. wiss. Bot., vol. 30, 1897, p. 249. P. N. Schürhoff, Jahrb. f. wiss. Bot., vol. 57, 1917, p. 363.

The Larger Non-living Inclusions of the Protoplasts.

20. H. Molisch, Mikrochemie der Pflanze, 3. Aufl., Jena 1923. O. Tunmann, Pflanzenmikrochemie, Berlin 1913. A. Meyer, cf. under 4.

21. J. Dekker, Die Gerbstoffe, Berlin 1913. K. Freudenberg, Die Chemie der natürlichen Gerbstoffe, Berlin 1920. *Id.*, Naturwissenschaften, vol. 8, 1920, p. 903.

22. M. Möbius, Farbstoffe der Pflanzen, Handb. d. Pflanzenanatomie, III., Berlin 1927.

23. A. Tschirch, Die Harze und die Harzbehälter 1900.

24. A. Frey, Vierteljahrsschr. Naturf. Gesellsch, Zürich, vol. 70, 1925.

25. Literature in A. Guilliermond and J. Beauverie, Ann. des sc. nat. Bot., IX. Sér., vol. 8, 1908, p. 173. S. Posternack, Compt. rend. Acad. scienc., Paris, vol. 169, 1919, p. 138.

26. C. Nägeli, Die Stärkekörner 1858. A. F. W. Schimper, Bot. Ztg. 1881, p. 223. E. T. Reichert, The Differentiation and specificity of starches, etc., Carneg. Inst. Washington Publ. No. 173, I, II, 1913. O. L. Sponsler, Americ. journ. of bot., vol. 9, 1922, p. 471. A. Meyer, Unters. über die Stärkekörner, 1895. H. Pringsheim, Landwirtsch. Versuchsstationen, vol. 84, 1914, p. 267. *Ib.*, cited in 29. J. J. Lynst-Zwikker, Rec. trav. bot. néerland, vol. 18, 1921, p. 1.

27. C. van Wisselingh, Die Zellmembran, Handb. d. Pflanzenanatomie, III, Berlin 1925.

28. E. Hannig, Flora, vol. 102, 1911, p. 209.

29. C. G. Schwalbe, Die Chemie der Zellulose, 2. Aufl., Berlin 1918. H. Pringsheim, Die Polysaccharide, 2. Aufl., Berlin 1923. E. Heuser, Lehrb. d. Zellulosechemie, 2. Aufl., Berlin 1923.

30. F. Ehrlich, Ztschr. f. angewandte Chemie, vol. 40, 1927, p. 1305.

31. B. Lee, Ann. of bot., vol. 39, 1925, p. 755.

32. A. Frey, Ber. deutsch. Bot. Gesellsch., vol. 44, 1926, p. 564. *Ib.*, Jahrb. f. wiss. Bot., vol. 65, 1925, p. 195; vol. 67, 1927, p. 597.

Section II. HISTOLOGY

33. A. de Bary, Comp. Anat. of the Vegetative Organs of the Phanerogams and Ferns 1884 (1877). G. Haberlandt, Physiologische Pflanzenanat., 6. Aufl. 1924. H. Solereder, Syst. Anat. d. Dikotyledonen 1899; W. Rothert, Gewebe, Handw. d. Naturwiss., IV, Jena 1913, p. 1144. E. Strasburger, cited in 7. A. Meyer, Erstes mikroskop. Praktikum, 3. Aufl., Jena 1915.

34. For the abundant literature cf. in 4.

35. O. Schüepp, Meristeme, Handb. d. Pflanzenanatomie, IV, Berlin 1926.

36. G. Krabbe, Das gleitende Wachstum bei der Gewebebildung der Gefaßpflanzen, Berlin 1886. F. Neef, Ztschr. f. Bot., vol. 6, 1914, p. 465.

37. L. Diels, Flora., vols. 111, 112, 1918, p. 490

38. R. Cunze, Beih. bot. Zentralbl., vol. 42, I, 1925, p. 160.

39. F. Netolitzky, Anatomie d. Angiospermen-Samen, Handb. d. Pflanzenanatomie, X, Berlin 1926.

40. E. Strasburger, Jahrb. f. wiss. Bot., vol. 5, 1866, p. 297. S. Schwendener, Monatsber. d. Berl. Akad. d. Wiss. 1881, p. 883. S. H. Eckerson, Bot. Gaz., vol. 46, 1908, p. 221. W. Zimmermann, Ztschr. f. Bot., vol. 19, 1927, p. 129.

41. A. Nestler, Ber. deutsch. bot. Gesellsch., vol. 43, 1925, p. 497.

42. G. Haberlandt, Die Sinnesorgane im Pflanzenreich, 2. Aufl. 1906.

43. G. Mylius, Biblioth. botan., Heft 79, 1912. H. Ziegenspeck, Ber. deutsch. bot. Gesellsch., vol. 39, 1921, p. 302. O. Hosbach, Beitr. z. Biologie d. Pflanzen, vol. 16, 1928, p. 81.

44. S. Schwendener, Das mechanische Prinzip im Bau der Monokotylen 1874. H. Ambronn, Jahrb. f. wiss. Bot., vol. 12, 1879. H. Puchinger, Sitzungsber. Akad. Wiss. Wien, math.-nat. Kl. I, vol. 131, 1922, p. 47. W. Rasdorsky, Ber. deut. bot. Gesellsch., vol. 44, 1926, p. 175; vol. 46, 1928, p. 48.

45. A. W. Hill, Ann. of Bot., vol. 15, 1901, p. 575, and vol. 22, 1908, p. 245.

A. F. HEMENWAY, Bot. Gazette, vol. 55, 1913, p. 236. E. W. SCHMIDT, Bau u. Funktion der Siebröhre, etc., Jena 1917. C. T. POPESCU, Ann. scientif. Univ, Jassy, XI, p. 135. E. KASTENS, Mitteil. Inst. f. allg. Bot. Hamburg, vol. 6, 1924, p. 33.

46. W. ROTHERT, Abhandlungen d. Akad. d. Wiss. Krakau 1899, p. 433. R. BAECKER, Sitzungsber. Akad. Wiss. Wien, math.-nat. Kl. I, vol. 131, 1922, p. 139. H. MOOG, Beih. bot. Zentralbl., vol. 42, I, 1925, p. 186.

47. H. MOLISCH, Studien über Milchsaft u. Schleimsaft der Pflanzen 1901.

48. M. NIEUWENHUIS-V. UEXKÜLL-GÜLDENBAND, Rec. trav. bot. néerland., vol. 11, 1914, p. 291.

SECTION III. ORGANOGRAPHY.

49. K. GOEBEL, Vergleichende Entwicklungsgeschichte der Pflanzenorgane 1883; and Organographie der Pflanzen, 3. Aufl., vol. 1, 1928; 2. Aufl., vol. 2, 1915–18; vol. 3, 1922–23. J. VELENOVSKY, Vergleichende Morphologie der Pflanzen, vol. 4, Prag 1905–1914. KERNER VON MARILAUN-HANSEN, Pflanzenleben, 3. Aufl., vol. 2, 1913. F. PAX, Allgemeine Morphologie der Pflanzen 1890.

50. A. FREY, Flora, vol. 120, 1926, p. 37.

Structure of the Thallus.

51. F. OLTMANNS, Morphologie u. Biologie der Algen, 2. Aufl. 1922. A. DE BARY, Comparative Morphology and Biology of the Fungi 1887 (1884).

52. F. SCHÜTT, Das Pflanzenleben d. Hochsee 1893.

53. E. DE WILDEMAN, Mém. couronnés et publiés par l'Acad. des sciences de Belgique, vol. 53, 1893.

54. H. LEITGEB, Untersuchungen über die Lebermoose, vols. 1-6, 1874–1879. K. GOEBEL, Organographie, 2. Aufl., vol. 2, Jena 1915. D. H. CAMPBELL, The structure and development of Mosses and Ferns, Ed. 3, 1918. TH. HERZOG, Anatomie d. Lebermoose, Handb. d. Pflanzenanatomie, VII, Berlin 1925.

Structure of the Typical Cormus.

55. Cf. works cited under 49.

56. M. RACIBORSKI, Spross. Handw. d. Naturwiss., vol. 9, p. 345, Jena 1913.

57. W. ZIMMERMANN, Jahrb. f. wiss. Bot., vol. 68, 1928, p. 289. P. RÖSSLER, Planta, vol. 5, 1928, p. 28.

58. W. HOFMEISTER, Allgemeine Morphologie der Gewächse, Leipzig 1868. M. HIRMER, Zur Lösung des Problems der Blattstellungen, Jena 1922.

59. S. SCHWENDENER, Mechanische Theorie der Blattstellungen 1878, and numerous papers in the Sitzungsber. d. Akad. d. Wiss. Berlin. HANS WINKLER, Jahrb. f. wiss. Bot., vol. 36, 1901, p. 1, and vol. 38, 1903, p. 501, contains further literature.

60. See works cited under 38.

61. E. STRASBURGER, Über den Bau und die Verrichtung der Leitungsbahnen in den Pflanzen 1891, pp. 98, 297. G. CHAUVEAUD, Ann. d. scienc. nat., Bot. IX sér., vol. 13, 1911, p. 113. F. J. MEYER, Progr. rei bot., vol. 5, 1917, p. 521.

62. M. BUCHHOLZ, Flora, vol. 114, 1921, p. 119.

63. J. C. SCHOUTE, Die Stelärtheorie 1902. H. SOLMS-LAUBACH, Bot. Ztg. 1903, II, Abt., pp. 37, 147. A. G. TANSLEY, New phytologist Nr. 2, 1908. F. J. MEYER, Beih. bot. Zentralbl., vol. 33, I, Abt. 1917. O. POSTHUMUS, Rec. trav. bot. néerland, vol. 21, 1924, p. 111.

64. K. GIESENHAGEN, Blatt, Handw. d. Naturwiss., vol. 2, 1912, p. 1.

65. v. DEINEGA, Flora, vol. 85, 1898, p. 439. M. HIRMER, Flora, vol. 113, 1920, p. 178.

66. F. J. MEYER, Assimilationsgewebe, Handb. d. Pflanzenanatomie, IV, Berlin 1923.

67. M. NORDHAUSEN, Ber. deutsch. bot. Gesellsch., vol. 30, 1912, p. 483.

68. E. NEUMANN-REICHARDT, Beitr. z. Allg. Bot., vol. 1, 1917, Heft 3.

69. K. DOMIN, Ann. d. jard. bot. Buitenzorg, vol. 24, 1911, p. 117. H. GLÜCK, Blatt- u. Blütenmorphol. Studien, Jena 1919.

70. E. BRICK, Beih. z. Bot. Zentralblatt, vol. 31, I, 1913, p. 209. P. NEESE, Flora, vol. 109, 1917, p. 144.

71. H. PFEIFFER, Pflanzl. Trennungsgewebe, Handb. d. Pflanzenanatomie, V, Berlin 1928.

72. M. RACIBORSKI, Handw. d. Naturwiss., vol. 9, 1913, Jena, p. 352.

73. W. SANDT, Zur Kenntnis de-Beiknospen, Bot. Abhandl., Heft 7, Jena 1925.

74. K. GOEBEL, Einleitung in die experimentelle Morphologie d. Pflanzen 1908, p. 165.

75. E. RÜTER, Flora, vol. 110, 1918, p. 195.

76. K. GIESENHAGEN, Wurzel, Handw. d. Naturwiss., vol. 10, p. 646, Jena 1915.

77. M. PLAUT, Festschr. z. 100 jähr. Bestehen d. Landw. Hochschule Hohenheim 1919, p. 129.

78. F. SCHWARZ, Unters. a. d. bot. Inst. in Tübingen, vol. 1, 1883, p. 135. E. S. WHITAKER, Bot. Gazette, vol. 76, 1923, p. 30.

79. K. KROEMER, Biblioth. botan., Heft 59, 1903. H. MÜLLER, Bot. Ztg., vol. 64, 1906, p. 53. M. PLAUT, Die physiol. Scheiden d. Gymnospermen. Equisetaceen u. Bryophyten, Diss. Marburg 1909; Mitteil. d. Kais.-Wilh.-Inst. f. Landw. Bromberg 1910, vol. 3, p. 63; Jahrb. f. wiss. Bot., vol. 28, 1910, p. 143.

80. G. RUMPF, Biblioth. bot., Heft 42, 1904.

81. G. CHAUVEAUD, Ann. d. scienc. nat. Bot., IX Sér., vol. 13, 1911, p. 113. A. GRAVIS, Bull. acad. roy. Belgique, Class. scienc. 1919, 4, p. 227. M. LENOIR, Ann. scienc. nat. Bot., X Sér., vol. 2, 1920, p. 1.

82. PH. VAN TIEGHEM, Traité de Bot., ed. 2, 1891, p. 700. Literature there cited.

83. FR. WETTSTEIN, Beih. z. bot. Zentralbl., vol. 20, II, 1906, p. 1.

84. K. GOEBEL, cited in 74.

85. M. BÜSGEN, Bau u. Leben unserer Waldbäume, 3. Aufl., Jena 1927. H. LUNDEGARDH, Kungl. Svensk. Vet. Akad. Handl., vol. 56, 1916, Nr. 3.

86. FR. HILDEBRAND, Engl. Bot. Jahrb. f. Syst. etc., vol. 2, 1882, p. 51.

87. J. C. SCHOUTE, Ann. jard. bot. Buitenzorg, 2. sér., vol. 11, 1912, p. 1. A. BORZI et G. CATALANO, Reale acad. d. Lincei, vol. 309, 1912, p. 167.

88. Cf. works under 33 and STRASBURGER under 61. E. C. JEFFREY, The anatomy of woody plants, Chicago 1917.

89. J. J. BEIJER, Rec. trav. bot. néerland, vol. 24, 1927, p. 633.

90. S. KOSTYTSCHEW, Ber. deutsch. bot. Gesellsch., vol. 40, 1922, p. 297.

91. E. ANTEVS, Progr. rei bot., vol. 5, 1917, p. 285.

92. O. GERTZ, Lund's univers. arsskrift N. F. II, vol. 12, 1916.

93. H. JANSSONIUS, De tangentiale groei van eenige pharm. Basten. Diss. Groningen 1918.

94. P. BÄSICKE, Bot. Ztg., 1908, p. 55.

95. E. KÜSTER, Pathologische Pflanzenanatomie, 3. Aufl. 1925.

Adaptations of the Cormus to its Mode of Life and to the Environment.

96. K. GOEBEL, Pflanzenbiologische Schilderungen, Marburg 1889–1893. F. A. W. SCHIMPER, Plant-Geography upon a Physiological Basis 1903 (1898). FR. W. NEGER, Biologie d. Pflanzen, Stuttgart 1913. G. KARSTEN, etc., Lehrb. d. Biol., 2. Aufl., Leipzig 1914. E. WARMING-P. GRAEBNER, Lehrb. d. ökolog. Pflanzengeographie, 3. Aufl., Berlin 1918. H. FITTING, Die ökolog. Morphologie d. Pflanzen, Jena 1926, and the works cited under 49.

97. H. SCHENCK, Biologie der Wassergewächse, Bonn 1886. K. GOEBEL, Pflanzenbiolog. Schilderungen 1891, vol. 2, p. 215. H. GLÜCK, Untersuchungen über Wassergewächse, 3., Jena 1905–11. H. SCHENCK, Wasserpflanzen, Handw. d. Naturwiss., vol. 10, p. 511, Jena 1905.

98. E. SCHREIBER, Österr. bot. Ztschr., vol. 71, 1922, p. 87.

99. J. SHREVE, Journ. of ecology, vol. 2, 1914, p. 82.

100. R. MARLOTH, Das Kapland, Wiss. Ergebn. d. deutsch. Tiefsee-Expedit., II, Teil 3, Jena 1908. O. RENNER, Flora, vol. 100, 1910, p. 451. MARLOTH, Flora des Kaplandes. H. FITTING, Ztschr. f. Bot., vol. 3, 1911, p. 109. A. ENGLER, Sitzungsber. kgl. preuß. Akad. d. Wiss. 1914, p. 564. O. RENNER, Xerophyten, Handw. d. Naturwiss., vol. 10, p. 664, Jena 1915. Numerous works on xerophytes of American deserts in the Publicat. of the Carnegie Inst. Washington. A. BURGERSTEIN, Die Transpiration der Pflanzen, II, Jena 1920, p. 181.

101. E. Warming, Mém. acad. royal d. scienc. de Danemark, 8. Sér., vol. 2, 1918, p. 297.

102. H. Schenck, Beitr. z. Biol. u. Anatomie d. Lianen, Jena 1892–93. H. Schenck, Lianen, Handw. d. Naturwiss., vol. 6, p. 176, Jena 1912. H. Pfeiffer, Abnormes Dickenwachstum, Handb. d. Pflanzenanatomie, IX, Berlin 1926.

103. K. Goebel, Pflanzenbiologische Schilderungen, vol. 1, p. 147. A. F. W. Schimper, Die epiphytische Vegetation Amerikas, Jena 1888. G. Karsten, Epiphyten, Handw. d. Naturwiss., vol. 3, p. 673, Jena 1913.

104. Ch. Darwin, Insectivorous Plants, 1876. K. Goebel, Pflanzenbiologische Schilderungen 1893, vol. 2. Clautriau, Mém. publ. par l'acad. de Belgique, vol. 59, 1900. G. Schmid, Flora, vol. 4, 1912, p. 335. F. W. Neger, Insektivoren, Handw. d. Naturwiss., vol. 5, p. 518, Jena 1914.

105. E. M. Merl, Flora, vol. 115, 1922, p. 59. A. Th. Czaja, Ztschr. f. Bot., vol. 14, 1922, p. 705.

106. L. Koch, Die Klee- u. Flachsseide, Heidelberg 1880. Peirce, Annals of Botany, vol. 8, 1894. Koch, Entwicklungsgesch. d. Orobanchen, Heidelberg 1887. H. Solms-Laubach, Rafflesiaceen in Engler, Das Pflanzenreich, Leipzig 1901. W. Benecke, Parasiten, Handw. d. Naturwiss., vol. 7, p. 497, Jena 1912. *Ib.*, Saprophyten, vol. 8, 1913, p. 559. K. Frhr. v. Tubeuf, Monographie der Mistel, München u. Berlin 1923. A. Sperlich, Absorptionsorgane d. parasit. Samenpflanzen, Handb. d. Pflanzenanatomie, IX, 2, Berlin 1925.

Organs of Reproduction.

107. The works cited under 49, 51, 53, and further Handw. d. Naturwiss., vol. 4, p. 171, Jena 1913.

108. H. Winkler, Verbreitung u. Ursache d. Parthenogenesis im Pflanzen- u. Tierreich, Jena 1920. W. N. Steil, Bot. Gazette, vol. 59, 1915, p. 254.

109. H. Winkler, Progr. rei bot., vol. 2, 1908, p. 293. A. Ernst, Ztschr. f. indukt. Abstammungslehre, vol. 17, 1917, p. 203. *Id.*, Bastardierung als Ursache der Apogamie im Pflanzenreiche, Jena 1918.

110. Th. H. Morgan, Die stoffliche Grundlage der Vererbung, Berlin 1921, p. 66.

111. H. Kylin, Ztschr. f. Bot., vol. 8, 1916, p. 545. O. Renner, Biolog. Zentralbl., vol. 36, 1916, p. 337. J. Buder, Ber. deutsch. bot. Gesellsch., vol. 34, 1916, p. 559. N. Svedelius, Ber. deutsch. bot. Gesellsch., vol. 39, 1921, p. 178.

Section IV. THE THEORY OF DESCENT AND THE ORIGIN OF ADAPTATIONS

112. Ch. Darwin, On the origin of species by means of natural selection, 1859. Ch. Darwin, Animals and Plants under Domestication. Ch. Darwin, The Descent of Man. E. Haeckel, Generelle Morphologie. Neudruck, Berlin 1906. *Ib.*, Natürliche Schöpfungsgeschichte, 10. Aufl. A. Weismann, Vorträge über die Deszendenztheorie, 3. Aufl., Jena 1913. J. P. Lotsy, Vorlesungen über Deszendenztheorien, Jena 1906. L. Plate, Der gegenwärtige Stand der Abstammungslehre, Leipzig 1909. Abel, Brauer, etc., Abstammungslehre, 12 Vorträge, Jena 1911. K. C. Schneider, Einführung in die Deszendenztheorie, 2. Aufl., Jena 1911. R. Hesse, Abstammungslehre und Darwinismus (Aus Natur und Geisteswelt, vol. 39), 6. Aufl., 1922. L. Plate, Deszendenztheorie, Handw. d. Naturwiss., vol. 2, p. 897, Jena 1912. J. Reincke, Kritik d. Abstammungslehre, Leipzig 1920. R. Hertwig, Abstammungslehre und neuere Biologie, Jena 1927.

113. J. Lamarck, Philosophie zoologique 1809. H. Spencer, The Principles of Biology. C. v. Nägeli, Mechanisch-physiologische Theorie der Abstammungslehre, München 1884. R. Semon, Die Mneme, 3. Aufl. 1911. A. Pauly, Darwinismus und Lamarckismus, München 1905. R. v. Wettstein, Der Neo-Lamarckismus, Jena 1903. *Ib.*, Handb. d. system. Botanik, Leipzig u. Wien, 3. Aufl. 1924, p. 39. O. Hertwig, Das Werden der Organismen, 3. Aufl., Jena 1922. C. Detto, Die Theorie der direkten Anpassung, Jena 1904.

114. G. Romanes, Darwin and after Darwin. L. Plate, Selektionsprinzip und Probleme der Artbildung, 3. Aufl., Leipzig 1908. A. Weismann, Die Selektionstheorie, Jena 1909. C. Detto, Die Theorie der direkten Anpassung, Jena 1904.

PHYSIOLOGY BY H. SIERP

1. The fullest exposition of plant physiology is to be found in W. Pfeffer's Pflanzenphysiologie, 2. Aufl. (2 vols.), Leipzig 1897–1904 (Eng. Trans. 1900–1906). This deals with the literature from 1897–1904, and the more important further literature is given below. Benecke-Jost, Pflanzenphysiologie (2 vols.), Jena 1923–1924.

2. Molisch (1897). Das Erfrieren der Pflanzen, Jena. Mez (1905), Flora 94. Winkler (1913), Jahrb. f. wiss. Bot., vol. 52, 1913. Maximow, *ib.*, vol. 53, 1914. Kylin, Ber. d. deutsch. bot. Ges., vol. 35, 1917. The significance of temperature for the geographical distribution of plants is fully treated in Schimper, Plant-Geography 1903 (1898). Solms-Laubach, Gesichtspunkte der Pflanzengeographie, Leipzig, 1905. Ihnes phänologische Karte des Frühlingseinzuges in Mitteleuropa (Petermanns Mitt. 1905, Heft 5). Becquerel, Compt. rend. Paris, vol. 148, 1909 ; vol. 150, 1910. Neuberger, Bot. Zentralbl., vol. 126, 1914, p. 665 (Ref.). Estreicher-Kiersnowska, *ib.*, vol. 134, p. 244 (Ref.). Zacharowa, Jahrb, wiss. Bot., vol. 65, 1926. Walter, Einführungen in die allgem. Pflanzengeographie Deutschlands 1927. Rawitscher, Die heimische Pflanzenwelt in ihrer Beziehung zu Landschaft, Klima und Boden 1927.

METABOLISM

3. Czapek, Biochemie der Pflanzen, Jena 1905 (2. Aufl. 1913–1921). Euler, Grundlagen und Ergebnisse der Pflanzenchemie, Braunschweig 1908. Nathansohn, Stoffwechsel der Pflanzen, Leipzig 1910. Grafe, Ernährungsphysiologisches Praktikum der höheren Pflanzen, Berlin 1914. Kostytschew, S., Pflanzenphysiologie, vol. 1, Berlin 1926.

Chemical Composition of the Plant.

4. E. Wolf, Aschenanalysen von land- und forstwirtschaftlichen Produkten, Berlin 1871, 1880. König, Zusammensetzung der menschlichen Nahrungs- und Genussmittel, Berlin 1882. Wehmer, Die Pflanzenstoffe, Jena 1911. Grafe, Chemie der Pflanzenzelle, Berlin 1922. Rosenthaler, Grundzüge der chemischen Pflanzenuntersuchung, Berlin 1923

Food Materials from the Soil.

5. Knop, Landw. Versuchsstationen, vol. 3, 1861. Appel, Ztschr. f. Bot., vol. 10, 1918. Shire, Amer. Journ. of bot., vol. 2, 1915. Livingston and Tottingham, *ib.*, vol. 5, 1918. Pringsheim, Abderhaldens Handb. biol. Arbeitsmethoden, vol. 11, 2, p. 645, 1920–22.

6. Arrhenius, Bodenreaktion und Pflanzenleben, Stockholm 1922. Michaelis, Wasserstoffionenkonzentration I, Berlin 1922–27. Olsen, C., Compt. rend. trav. du Laborat. Carlsberg 15, 1923. Bresslau, Die Bedeutung der Wasserstoffionenkonzentration für die Hydrobiologie, 1926.

7. Mevius, Naturw. u. Landw., Freising-München 1927. Wehrle, Ztschr. f. Bot., vol. 19, 1927, p. 209. Zollitsch, Flora, vol. 22, 1927, p. 93.

8. Stocker, Ergebnisse der Biologie, vol. 3, 1928, p. 265-353.

9. Stoklasa, Verbreitung des Aluminiums in der Natur, Jena 1922.

10. Adolf Mayer, Agrikulturchemie, 5. Aufl., Heidelberg 1901.

11. Schimfer, Plant-Geography upon a Physiological Basis 1903 (1898). Engler, Vers. einer Entwicklungsgeschichte der Pflanzenwelt, Leipzig 1879–82. Solms-Laubach, Die leitenden Gesichtspunkte d. Pflanzengeographie, L. 1905. Beitr. z. Biologie, vol. 13. Walter and Rawitscher, see No. 8.

The Absorption and Movement of the Nutrient Salts in the Green Plant.

12. Walter, Der Wasserhaushalt der Pflanze, Freising-München 1925. Huber, Jahrb. f. wiss, Bot., vol. 64, 1925.

13. Pfeffer, Osmotische Untersuchungen, Leipzig, 1877. Höber, Physik. Chemie der Zelle, 6. Aufl., 1926.

14. Rippel, Ber. d. deutsch. bot. Ges., vol. 36, 1918. Hansteen-Cranner, Ber. d. deutsch. bot. Ges., vol. 37, 1919. Denny, Bot. Gaz., vol. 63, 1917. Schroeder, Biol. Zentralbl., vol. 42, 1922.

15. Ursprung and Blum, Biol. Zentralbl., vol. 40, 1920. Renner, Jahrb. f. wiss. Bot., vol. 56, 1915. Ursprung, Ber. d. deutsch. bot. Ges., vol. 41, 1923, p. 338. Ursprung and Blum, Jahrb. f. wiss. Bot., vol. 63, 1924, p. 1. Ursprung, Planta, vol. 2, 1926, p. 640. Ursprung and Blum, Jahrb. f. wiss. Bot., vol. 65, 1926, p. 1.

15*a*. A table of the osmotic pressures of various concentrations of sugar in Ursprung, Ber. d. deutsch. bot. Ges., vol. 34, 1916, p. 533

16. Blum, Beih. bot. Zentralbl. I, vol. 33, 1916. *Id.*, Beih. bot. Zentralbl., vol. 43, 1926, p. 1. Höfler, Planta, vol. 2, 1926, p. 454. Turesson, Jahrb. f. wiss. Bot., vol. 66, 1927, p. 723.

17. Eschenhagen, Diss. Leipzig 1889. Lepeschkin, Ber. d. deutsch. bot. Ges., vol. 28, 1910. Tröndle, Jahrb. f. wiss. Bot., vol. 48, 1910. Fitting, Jahrb. f. wiss. Bot., vol. 56, 1915. Blum, see **16**. Turesson, see **16**.

18. Nägeli, Pflanzenphysiol. Unters., vol. 3, 1858. Katz, Kolloidchem. Beihefte, vol. 9, 1916. Freundlich, Kapillarchemie, 2. Aufl. 1922.

19. Watler, Jahrb. f. wiss. Bot., vol. 62, 1923, p. 145. *Id.*, Ztschr. f. Bot., vol. 16, 1924, p. 353.

20. Fitting, Ztschr. f. Bot., vol. 3, 1911. Ursprung and Blum, Biol. Zentralbl., vol. 40, 1920.

21. Lundegårdh, Klima und Boden in ihrer Wirkung auf das Pflanzenleben, Jena 1925. Wahnschaffe and Schucht, Wissenschaftliche Bodenuntersuchungen. Berlin 1927. Bachmann, Planta, vol. 3, 1927, p. 1400. Lang, Forstliche Bodenuntersuchung, Webers Handb. d. Forstwiss., 1926.

22. Ruhland, Jahrb. f. wiss. Bot., vol. 46, 1908. *Ib.*, vol. 55, 1915. Fitting, Jahrb. f. wiss. Bot., vol. 56, 1915 ; vol. 57, 1917 ; vol. 59, 1919. Höfler, Ber. d. deutsch. bot. Ges., vol. 36, 1918; vol. 37, 1919. Tröndle, Arch. sc. phys., vol. 45, 1918. Klebs, Sitzber. Heidelberger Akad., 1919. Höber, Physikal. Chemie der Zelle. 6. Aufl., Leipzig 1926. Höfler and Weber, Jahrb. f. wiss. Bot., vol. 65, 1926, p. 643. de Visser Smits, Rec. trav. bot. néerl., vol. 23, 1926, p. 104.

23. Pfeffer, Unters. bot. Inst. Tübingen, vol. 2, 1886. Ruhland, Jahrb. f. wiss. Bot., vol. 54, 1914. Küster, Jahrb. f. wiss Bot., vol. 50, 1911. Wisselingh, Beih. bot. Zentralbl. (I), vol. 32, 1914. Schaede, Jahrb. f. wiss. Bot., vol. 62, 1923, p. 65.

24. Overton. Jahrb. f. wiss. Bot., vol. 34, 1900. Boas, Ber. d. deutsch. bot. Ges., vol. 40, 1922, p. 32. Lepeschkin, Biochem. Ztschr., vol. 139, 1923, p. 280. Höber, see No. 22, 1926. Collander and Bärlund, Soc. Sc. Fenn. Comm. Biol., vol. 2, 1926, p. 9. Grafe, Naturwiss., vol. 15, 1927, p. 513. Collander, Protoplasma, vol. 3, 1928.

25. Ruhland, Jahrb. f. wiss. Bot., vol. 51, 1912. Collander, *Ibid.*, vol. 60, 1921. *Id.*, Kolloidchem. Beihefte, vol. 20, 1924, p. 273. Ruhland, Planta, vol. 1, 1926, p. 1.

26. Traube, Pflügers Archiv, vol. 105, 1904 ; vol. 123, 1908. Czapek, Methode zur direkten Bestimmung der Plasmahaut, Jena 1911. Dorner, Bakt. Zentralbl. II, vol. 56, 1922, p. 14. Metzner, Chem. Ztg., vol. 53, 1923.

27. Hansteen, Med. fr. Norges Landbrucksh, vol. 1, 1922. Hansteen-Cranner, Planta, vol. 2, 1926, p. 438. Grafe, Naturwissenschaften, vol. 15, 1927.

28. Kunze, Jahrb. f. wiss Bot., vol. 42, 1906. Bachmann, Ber. d. deutsch. bot. Ges., vols. 22-29. Schulow, Ber. d. deutsch. bot. Ges., vol. 31, 1913.

29. Burgerstein, Transpiration der Pflanzen, Jena 1904, 1920. Renner, Flora, vol. 100, 1910. *Id.*, Ber. d. deutsch. bot. Ges., vol. 30, 1912 ; Handw. d. Naturwiss., vol. 10, 1913, p. 538. Huber, Jahrb. f. wiss. Bot., vol. 64, 1925, p. 1.

30. Iljin, Biochem. Ztschr., vol. 132, 1922. Steinberger, Biol. Zentralbl., vol. 42, 1922. Iljin, Jahrb. f. wiss. Bot. 1922, pp. 670, 696. Arends, Planta, vol. 1, 1926, p. 84. Stålfeld, Flora, vol. 21, 1927, p. 236.

31. Höhnel, Mitteil. a. d. forstl. Versuchswesen Österreichs, vol. 2, 1879–80. Briggs and Shantz, Journ. of agric. research, vols. 3, 5, 1914, 1916.

32. Livingston, Carnegie-Inst. Publ., vol. 50, 1906. Renner, see No. **16**, 1913.

Walter, Ztschr. f. Bot., vol. 18, 1926, p. 1. Sierp and Seybold, Planta, vol. 3, 1927, p. 115. Seybold, Planta, vol. 4, 1927.

33. Stahl, Bot. Ztg., vol. 52, 1894. Stein, Ber. d. deutsch. bot. Ges., vol. 30, 1912. Molisch, Ztschr. f. Bot., vol. 4, 1912. Neger, Ber. d. deutsch. bot. Ges., vol. 30, 1912. *Id.*, Flora, vol. 111, 1919. Fr. Weber, Ber. d. deutsch. bot. Ges., vol. 34, 1916. Darwin, Proceed. R. Soc. B., vol. 84, 1911. On the self-registering porometer, cf. Pinkhof, Akad. Amsterdam 1920. Dietrich, Jahrb. f. wiss. Bot., vol. 65, 1926, p. 98. Leick, Jahrb. f. wiss. Bot., vol. 67, 1927.

34. Wieler, Cohns Beitr. z. Biol., vol. 6, 1893. Ruhland, Jahrb. f. wiss. Bot., vol. 53, 1915. Faber, v., Jahrb. f. wiss. Bot., vol. 56, 1915. Stahl, Flora, vol. 111, 1919. Montfort, Jahrb. f. wiss. Bot., vol. 59, 1920, p. 467. Lippmann, Bot. Arch., vol. 11, 1925, p. 361.

35. Lepeschkin, Beih. bot. Zentralbl., vol. 19, 1906. Pfeffer, Abh. Ges. d. Wiss., Leipzig 1890. Priestley, New Phytolog., vol. 21, 1922, p. 41. Schaposchnikow, Beih. bot. Zentralbl., vol. 43, 1926, p. 133.

36. Renner, Handw. d. Naturwiss., vol. 10, 1913. "Wasserversorgung." Ewart, Philos. Transact. Roy. Soc. (B), vol. 199, 1908. *Id.*, Annals of Bot., vol. 24, 1910. Huber, Ber. d. deutsch. bot. Ges., vol. 43, 1925, p. 410.

37. Renner, Ber. d. deutsch. bot. Ges., vol. 36, 1918. Nordhausen, Jahrb. f. wiss. Bot., vol. 58, 1917. *Id.*, Ber. d. deutsch. bot. Ges., vol. 37, 1919. Renner, Flora, vol. 103, 1911. *Id.*, Jahrb. f. wiss. Bot., vol. 56, 1915. Ursprung, Ber. d. deutsch. bot. Ges., vol. 33, 1915; vol. 34, 1916. Stern, Ber. d. deutsch. bot. Ges., vol. 44, 1926, p. 470.

38. Huber, Ber d. deutsch. bot. Ges., vol. 42, 1924, p. 27.

39. Holle, Flora, vol. 108, 1915. Bode, Jahrb. f. wiss. Bot., vol. 62, 1923, p. 92. Huber, Biol. Zentralbl., vol. 43, 1923, p. 30.

The Nutrient Materials derived from the Atmosphere.

40. Claussen, Flora, vol. 88, 1901. Lindner, Beiträge z. Biologie 13, 1916. Schroeder, Flora, vol. 17, 1924, p. 270. Romell, Flora, vol. 21, 1926, p. 125.

The Assimilation of the Food Materials in the Green Plant.

41. Willstaetter and Stoll, Unters. über Assimilation der Kohlensäure, 1918. Wislicenus, Ber. chem. Ges., vol. 51, 1918. H. Schröder, Die Hypothesen über die chem. Vorgänge bei der Kohlensäure-assimilation, 1917; Ber. d. deutsch. bot. Ges., vol. 36, 1918. Kostytschew, Ber. d. deutsch. bot. Ges., vol. 40, 1922, p. 112; Ber. d. deutsch. bot. Ges., vol. 41, 1923, p. 277. Johannson, Svensk. bot. Tidskr., vol. 17, 1923, p. 215. Otto, Naturwiss., vol. 13, 1925, p. 985. Bredler, Bot. Arch., vol. 20, 1927, p. 143.

42. Kniep and Mindler, Ztschr. f. Bot., vol. 3, 1909. Ursprung. Ber. d. deutsch. bot. Ges., vol. 36, 1918.

43. Brown, Proc. R. Soc. (B), vol. 76, 1905. Puriewitsch, Jahrb. f. wiss. Bot., vol. 53, 1914.

44. Wurmser, Recherches sur l'assimilation chlorophyllienne, 1921. Warburg, Ztschr. f. physik. Chemie, vol. 102, 1922. Warburg and Negelein, Naturwiss., vol. 10, 1922, p. 647. *Id.*, Ztschr. physikal. f. Chemie, vol. 102, 1922, p. 235. Warburg, Ztschr. f. physikal. Chemie, vol. 106, 1923, p. 191.

45. Willstaetter and Stoll, Sitzungsber. Berl. Akad., 1915. Willstaetter, see No. 41. Noack, Ztschr. f. Bot., vol. 17, 1925, p. 481.

46. Schröder, Die Naturwissenschaften, 1919. *Id.*, Die Stellung der grünen Pflanze im irdischen Kosmos, Berlin 1920. Lundegardh, Kreislauf der CO_2 in der Natur, Jena 1924.

47. Bornemann, Kohlensäure und Pflanzenwachstum, Berlin 1920. Hugo Fischer, Angew. Bot., vol. 2, 1920; vol. 3, 1921. Kisselew, Beitr. bot. Zentralbl. (I), vol. 32, 1915.

48. Mitscherlich, Landw. Jahrb., vol. 38, 1909. *Id.*, Ztschr. f. Pflanzenernährung u. Düngung, vol. 1, 1922. Benecke, Ztschr. f. Bot., vol. 13, 1921. Harder, Jahrb. f. wiss Bot., vol. 60, 1921. Lundegårdh, Biol. Zentralbl., vol. 42, 1922. Harder, Ztschr. f. Bot., vol. 15, 1923, p. 305.

49. Blackman, Annals of Bot., vol. 19, 1905. *Id.*, Proc. Roy. Soc. (B), vol. 76. Thoday, Proc. Roy. Soc. (B), vol. 82, 1910.

50. WARBURG and NEGELEIN, Biochem. Ztschr., vol. 110, 1920, have studied the assimilation of nitric acid by new methods. It may be noted that they placed the plants under investigation in a solution of n/10 NaHO$_3$ + n/100 HNO$_3$, which is generally regarded as poisonous. MUENSCHER, Bot. Gaz., vol. 75, 1923, p. 249. ULLRICH, Ztschr. f. Bot., vol. 16, 1924, p. 513.

51. RUHLAND and WETZEL, Planta, vol. 1, 1926, p. 558. MOTHES, Planta, vol. 1, 1926, p. 472; Ber. d. deutsch. bot. Ges., vol. 45, 1927, p. 472.

Translocation and Transformation of Assimilates in the Green Plant.

52. BIEDERMANN, Fermentforschung, vol. 1, 1916; vol. 4, 1920. WILLSTAETTER Ber. chem. Ges., vol. 55, 1922. EULER, Ib., 1920.

53. WALDSCHMIDT-LEITZ, Die Enzyme, Wirkungen und Eigenschaften, 1926. BLEDIG, Anorgan. Fermente Leipzig 1891. HÖBER, see No. 9. EULER, Chemie der Enzyme, 2. Aufl., 1920 and 1921. II. Teil: Spezielle Chemie der Enzyme. München and Wiesbaden 1922.

54. KARRER, Ergebn. d. Physiol., vol. 20, 1922, and Naturwiss., vol. 9, p. 399. FLIEG, Jahrb. f. wiss. Bot., vol. 61, 1922, p. 24. PRIESTLEY, New Phytolog., vol. 23, 1924. COSTER, Ann. jard. bot. Buitenzorg, vol. 35, 1926, p. 71.

55. DELEANO, Jahrb. f. wiss. Bot., vol. 49, 1911. TEODORESKO and POPESCO, Annal. sc. de l'univ. de Jassy, vol. 9. BIRCH-HIRSCHFELD, Jahrb. f. wiss. Bot., vol. 59, 1920, p. 171.

56. SWART, Stoffwanderung in ablebenden Blättern, Jena 1914.

57. CZAPEK and EULER, see No. 4. HANNIG, Ztschr. f. Bot., vol. 14, 1922, p. 385. ZIEGENSPECK, Bot. Arch., vol. 7, 1924, p. 171.

Heterotrophic Nutrition.

58. BOAS, Biochem. Ztschr., vol. 86, 1918. TREBOUX, Ber. d. deutsch. bot. Ges., vol. 30, 1912. NOACK, Ztschr. f. Bot., vol. 14, 1922, p. 1. BRANNON, Bot. Gaz., vol. 76, 1923, p. 257.

59. WINOGRADSKI, Archives d. sc. biologiques, vol. 3, 1895. *Id.*, Zentralbl. f. Bakt. (II), vol. 9, 1902. KOCH, in LAFAR, Technische Mykologie, vol. 3, Jena 1904. HELLRIEGEL and WILFARTH, Stickstoffnahrung d. Gramineen u. Leguminosen, Berlin. HILTNER, in LAFAR, Technische Mykologie, vol. 3, Jena 1904. BREDEMANN, Zentralbl. f. Bakt. (II), vol. 23, 1909. KRZEMIENIEWSKI, Bull. acad. Cracovie, 1908. STOKLASA, Zentralbl. f. Bakt. (II), vol. 21, 1908. NIEMEYER, Bot. Arch., vol. 7, 1924, p. 347. FEHER and BOKAR, Planta, vol. 2, 1926, p. 406. KOSTYTSCHEW and SCHWEZOWA, Planta, vol. 2, 1926, p. 527.

60. LAWES, GILBERT, and PUGE, Philos. Transact., vol. 151, 1862. SCHULTZ-LUPITZ, Landw. Jahrb., vol. 10, 1881.

61. STAHL, Jahrb. f. wiss. Bot., vol. 34, 1900. BERNARD, Annales des sciences nat. (9), vol. 9, 1909. BURGEFF, Wurzelpilze der Orchideen, Jena 1909. WEYLAND, Jahrb. f. wiss. Bot., vol. 51, 1912. MIEHE, Flora, vol. 111, 1918. REXHAUSEN, Beitr. z. Biol., vol. 14, 1920. RAYNER, Ann. of Bot., vol. 29, 1915. SPRATT, *ib.*, vol. 29, 1915. BOTTOMLEY, *ib.*, vol. 29, 1915. DEMETER, Flora, vol. 16, 1923, p. 405. MELIN, Untersuchungen über die Bedeutung der Baummykorrhiza, Jena 1925. RAYNER, New Phytolog., vol. 25, 1926.

62. NIENBURG, Ztschr. f. Bot., vol. 9, 1917.

63. v. FABER, Jahrb. f. wiss. Bot., vol. 51, 1912. *Ib.*, vol. 54, 1914. MIEHE, *Ib.*, vol. 53, 1913; vol. 58, 1917.

64. HEINRICHER, Jahrb. f. wiss. Bot., vols. 31, 32, 36, 37, 46, 47. *Id.*, Naturwissenschaften, 1917. KOSTYTSCHEW, Ber. d. deutsch. bot. Ges., vol. 42, 1924, p. 363. *Id.*, Beih. bot. Zentralbl., vol. 40, 1924, p. 351.

65. DARWIN, Insectivorous Plants. GOEBEL, Pflanzenbiolog. Schilderungen, vol. 2, Marburg 1893. CLAUTRIAU, Mém. publ. p. l'acad. de Belgique, vol. 59, 1900. SCHMID, Flora, vol. 104, 1912. LÜTZELBURG, Flora, vol. 100, 1910. RUSCHMANN, Zur Ökologie von Pinguicula . . . Diss. Jena 1914. STERN, Flora, vol. 109, 1917. KOSTYTSCHEW, Ber. d. deutsch. bot. Ges., vol. 41, 1923, p. 277.

Respiration and Fermentation.

66. BUTKEWITSCH, Jahrb. f. wiss. Bot., vol. 64, 1925, p. 637. MAYER, Jahrb. f. wiss. Bot., vol. 65, 1926, p. 636. RUHLAND and WETZEL, Planta, vol. 1, 1926,

p. 558. Ullrich, Planta, vol. 1, 1926, p. 565. Wetzel, Planta, vol. 4, 1927, p. 476.

67. Pfeffer, Unters. bot. Inst. Tübingen, vol. 1, 1885. Johannsen, Unters. bot. Inst. Tübingen, vol. 1, 1885. Stich, Flora, vol. 74, 1891. Kostytschew, Ber. d. deutsch. bot. Ges., vol. 31, 1913. *Id.*, Pflanzenatmung, 1924.

68. Wieland, Ber. chem. Ges., vol. 46, 1913, p. 3. Palladin, Biochem. Ztschr., vol. 60, 1914. Wieland, see No. 67, 1922. The theory of respiration, defended by Nathansohn (1919, Kolloidchem., Beiheft), is fundamentally different. As supporters of the hypothesis of O-activation may be mentioned: Warburg, Naturwissenschaften, 1921. *Id.*, Biochem. Ztschr., vol. 136, p. 266; vol. 142, p. 518, 1923; and Naturwissenschaften, vol. 11, p. 862. Smirnow, Ber. d. deutsch. bot. Ges., vol. 44, 1926, p. 99.

69. Winogradski, Annales Inst. Pasteur, vol. 4, 1890; vol. 5, 1891. Hueppe, Ergebn. d. intern. bot. Kongr., Wien 1906. Krzemieniewski, Bull. acad. Cracovie, 1908. Niklewski, Jahrb. f. wiss. Bot., vol. 48, 1910. Lebedeff, Ber. d. deutsch. bot. Ges., vol. 27, 1909. Lieske, Jahrb. f. wiss. Bot., vol. 49, 1911. Keil, Beitr. z. Biol., vol. 11, 1912. Münz, Zur Phys. d. Methanbakterien, Diss. Halle 1915. Winogradski, Bot. Ztg., vol. 45, 1887; Ann. Inst. Pasteur, vol. 4, 1890; vol. 5, 1891. Niklewski, Bull. acad. Cracovie, 1907. Söhngen, Zentralbl. f. Bakt. (II), vol. 15, 1906. Lieske, Zentralbl. f. Bakt. (II), vol. 49, 1919. Meyerhof, Pflügers Archiv. f. Phys., vols. 164-166. Ruhland, Ber. d. deutsch. bot. Ges., vol. 40, 1922. *Id.*, Jahrb. f. wiss. Bot., vol. 63, 1924, p. 321. Baas-Becking, Ann. of Bot., vol. 39, 1925, p. 613. Cholodny, Eisenbakterien, Jena 1926.

70. Cf. Czapek, Euler, and Nathansohn in No. 3. Kruse, Mikrobiologie, 1910. Benecke, Bau u. Leben der Bakterien. L., 1912.

71. Buchner, E. and H., and Hahn, Die Zymasegärung, München 1903. Buchner, Biochemische Ztschr., 1908. Euler and Lindner, Chemie der Hefe und der alkohol. Gärung, Leipzig 1915.

72. Neuberg, Die Gärungsvorgänge und der Zuckerumsatz, Jena 1913. *Id.*, Ztschr. f. Bot., vol. 11, 1919. Neuberg, Ber. chem. Ges., vol. 55, 1922.

73. Brenner, Jahrb. f. wiss. Bot., vol. 57, 1917.

74. Molisch, Ztschr. f. Bot., vol. 6, 1914. Leick, Biol. Zentralbl., vol. 36, 1916.

75. Molisch, Leuchtende Pflanzen, 2. Aufl., Jena 1912. Buchner, Tier und Pflanze in intrazellulärer Symbiose, Berlin 1921.

DEVELOPMENT

76. Pfeffer, Physiologie, vol. 2, 1904. Winkler, Entwicklungsphysiologie in Handw. d. Naturwiss., vol. 3, Jena 1913. Küster, Pathol. Pflanzenanatomie, 2. Aufl., Jena 1916.

Commencement of Growth.

77. Gassner, Jahrb. f. wiss. Bot., vol. 55, 1915. Lehmann, Ztschr. f. Bot., vol. 5, 1913. *Ib.*, vol. 7, 1915. *Id.*, Ber. d. deutsch. bot. Ges., vol. 36, 1918. Ottenwälder, Ztschr. f. Bot., vol. 6, 1914.

78. Fischer, Ber. d. deutsch. bot. Ges., vol. 25, 1907.

79. Cf. Goebel, Exp. Morphologie, Leipzig 1908; Biol. Zentralbl., vol. 36, 1916. Winkler, cited in 63. Rao and Lehmann, Ber. d. deutsch. bot. Ges., vol. 42, 1924. Rao, Jahrb. f. wiss. Bot., vol. 64, 1925. Kommerell, Jahrb. f. wiss. Bot., vol. 66, 1927.

80. Johannsen, Atherverfahren b. Treiben, Jena 1906. Molisch, Das Warmbad, Jena 1909. Jesenko, Ber. d. deutsch. bot. Ges., vol. 30, 1912. Lakon, Ztschr. f. Bot., vol. 4, 1912. Müller-Thurgau and Schneider-Orelli, Flora, vols. 101, 104. Weber, Sitzungsber. Akad. Wiss., vol. 1, 1916, p. 125.

General Phenomena of Growth.

81. Karsten, Ztschr. f. Bot., vol. 7, 1915; vol. 10, 1918. Klebs, Sitzungsber. Heidelb. Akad., 1916–17. Stalfelt, Svensk, Vetenskap.-akad. Handlingar, vol. 62, 1921.

82. Haberlandt, Beitr. z. allgem. Bot., vol. 2, 1921.

83. Ursprung and Blum, Jahrb. f. wiss. Bot., vol. 63, 1924.

84. See literature in 81.

85. Koningsberger, Rec. trav. bot. néerl., vol. 24, 1922. Lundegardh, Arkiv för Bot., vol. 18, 1922. Buder, Ber. d. deutsch. bot. Ges., vol. 44, 1926.

Factors of Development.

86. Talma, Rec. trav. bot. néerl., vol. 15, 1918. Graser, Beitr. bot. Zentralbl. (I), vol. 36, 1919. Sierp, Biol. Zentralbl., vol. 40, 1920.

87. Blaauw, Ztschr. f. Bot., vol. 6, 1914; vol. 7, 1915. Vogt, Ztschr. f. Bot., vol. 7, 1915. Sierp, Ztschr. f. Bot., vol 10, 1918. *Id.*, *ibid.*, vol. 13, 1921. Brauner, Ztschr. f. Bot., vol. 14, 1922. Lundegardh, Arkiv för Bot., vol. 8, 1921.

88. Klebs, Sitzungsber. Heidelb. Akad., 1916-17. Trumpf, Bot. Arch., vol. 5, 1924. Hammer, Bot. Arch., vol. 14, 1926. Priestley, New Phytolog., vol. 24, 1925. Johannsen, Flora, vol. 21, 1927.

89. Klebs, Sitzungsber. Heidelb. Akad., math.-nat. Kl., 1917.

90. Körnicke, Jahrb. f. wiss. Bot., vol. 56, 1925. Esdorn, Diss. 1924. Iven, Strahlentherapie, vol. 19, 1925. Pekarek, Planta, vol. 4, 1927.

91. A. Engler, Tropismen und exzentr. Dickenwachstum, Zürich 1918. Rawitscher, Ztschr. f. Bot., vol. 15, 1923.

92. Rippel, Beih. bot. Zentralbl. (I), vol. 36, 1919. André, Ztschr. f. Bot., vol. 12, 1920.

93. Heumann, Bot. Arch., vol. 4, 1923. Trumpf, Bot. Arch., vol. 5, 1924. Wolkenhauer, Bot. Arch., vol. 6, 1924.

94. Küster, Die Gallen der Pflanzen. L., 1911. *Id.*, Pathol. Pflanzenanatomie, Jena 1916. Magnus, Entstehung der Gallen, Jena 1914. Molliard, Bot. Zentralbl., vol. 138, 1918 (Abs.).

95. Heinricher, Denkschr. Akad. Wiss. Wien., Math.-nat. Kl., vol. 93, 1916. Burgeff, Die Wurzelpilze der Orchideen, Jena 1909.

96. See No. 81.

97. Sierp, Jahrb. f. wiss. Bot., vol. 53, 1913. Kraus, Sitzungsber. phys. med. Ges. Würzburg, 1915.

97*a*. Wettstein, Ztschr. f. ind. Abst., vol. 33, 1924.

98. Nienburg, Wiss. Meeresunters., N. F., Helgoland 15, Nr. 7, 1922. *Id.*, Ber. d. deutsch. bot. Ges., vol. 40, 1922. Neeff, Jahrb. f. wiss. Bot., vol. 61, 1922. Lund, Bot. Gaz., vol. 76, 1923. Janse, Flora, vols. 118-119, 1925. Steinecke, Bot. Arch., vol. 12, 1925.

99. Voechting, Unters. z. exp. Anatomie u. Pathologie, Tübingen 1918. Kny, Ber. d. deutsch. bot. Ges., vol. 7, 1889.

100. Vöchting, Organbildung, Bonn 1878. Goebel, Biol. Zentralbl., vol. 22, 1902. Korschelt, Regeneration u. Transplantation, Jena 1907. Linsbauer, Denkschr. d. Akad. Wien, vol. 93, 1915. Ungerer (Die Regulation der Pflanzen, Berlin 1919) [Rouxs Vorträge 22] points out rightly that there is much confusion with regard to the various forms of restitution. The terms reparation and regeneration previously employed have therefore been omitted in the account in the text.

101. Hartsema, Rec. trav. bot. néerl., vol. 23, 1926. Figdor, Planta, vol. 2, 1926. Ossenbeck, Flora, vol. 22, 1927.

102. Goebel, Bot. Ztg., vol. 38, 1880. *Id.*, Experimentelle Morphologie, Leipzig 1908. Voechting, Die Transplantation, Tübingen 1892. *Id.*, Jahrb. f. wiss. Bot., vol. 16, 1885.

103. Winkler, Ber. d. deutsch. bot. Ges., vol. 26*a*, 1908. Buder, Ztschr. f. Abst., vol. 5, 1911. Winkler, Unters. über Pfropfbastarde, Jena 1912. Meyer, Ztschr. f. Abst., vol. 13, 1915. Noack, K. L., Jahrb. f. wiss. Bot., vol. 61, 1922.

104. Schroeder, Flora, vol. 99, 1909. Bose, Plant response, New York and Bombay 1906. Leitch, Annals of Bot., vol. 30, 1916. Walter, Ztschr. f. Bot., vol. 13, 1921. Arens, Ann. Jard. bot. Buitenzorg, vol. 32, 1923. Coster, *ibid.*, vol. 33, 1923. *Id.*, *ibid.*, vol. 35, 1926. Klebs, Sitzungsber. Heidelb. Akad. Wiss., math.-nat. Kl., vol. 2, 1926. *Id.*, *ibid.*, vol. 7, 1926.

105. Blaauw, Ztschr. f. Bot., vol. 6, 1914. *Id.*, Ztschr. f. Bot., vol. 7, 1915. Vogt, Ztschr. f. Bot., vol. 7, 1915. Blaauw, Med. v. Landbouwhoogeschool Wageningen, vol. 15, 1918. Sierp, Ztschr. f. Bot., vol. 10, 1918. *Id.*, *ibid.*, vol. 13, 1921. Tollenaar and Blaauw, Proc. Amsterd. Akad., vol. 24, 1921. Renner, Ztschr. f. Bot., vol. 14, 1922. Brauner, *ib.*, vol. 14, 1922. Lundegardh, Arkiv für Bot., vol. 18, 1922. Koningsberger, Rec. trav. bot. néerl., vol. 19, 1922.

Tollenaar, Proc. Amsterd. Akad., vol. 26, 1923. van Dillewijn, Rec. trav. bot. néerl., vol. 24, 1927. See also Probst, Planta, vol. 4, 1927.

Duration of Life.

106. Korschelt, Lebensalter, Altern und Tod, Jena 1917. Küster, Bot. Betr. über Alter und Tod. (Abh. z. theoret. Biologie, vol. 10), Berlin 1921.

107. Strasburger, Deutsche Rundschau, 1898–99. Schenck, Wiss. Ergebn. d. Tiefsee-Expedition, vol. 2, 3. Heft, Jena 1907. Kronfeld, Mitt. d. dendrol. Ges., 1920. Stuck, Ztschr. f. Ges. f. Erdkunde, 1923. Pütter, Naturwiss., vol. 14, 1926.

Reproduction.

108. Klebs, Willkürliche Entwicklungsänderungen, Jena 1903. *Id.*, Fortpflanzungsphysiologie nied. Organismen, Jena 1896.

109. Klebs, Flora, vol. 111, 1918. André, Schaxels Abhandl., vol. 20, 1926.

110. Noll, Sitzungsber, niederrh. naturf. Ges., 1902. Ewert, Parthenokarpie . . . der Obstbäume, Berlin 1907. Müller-Thurgau, Landw. Jahrb. d. Schweiz, 1908.

111. Fitting, Ztschr. f. Bot., vol. 1, 1909; vol. 2, 1910. *Id.*, Biol Zentralbl., vol. 29, 1909.

112. Another view in the abstract by Schellenberg, 15th Nov. 1907, in the Gesellschaft schweizerischer Landwirte.

113. Winkler, Progr. rei. bot., vol. 2, 1908; Verbreitung und Ursache der Parthenogenesis, Jena 1920. Strasburger, Zeitpunkt der Bestimmung des Geschlechts Apogamie, Parthenogenesis, etc., Jena 1909. Ernst, Bastardierung als Ursache der Apogamie, Jena 1918.

Heredity Variability, Origin of Species.

114. Correns, Die neuen Vererbungsgesetze, Berlin 1912. Baur, Einführung in die exp. Vererbungslehre, 3. Aufl., Berlin 1919. Goldschmidt, Der Mendelismus in elementarer Darstellung, Berlin 1920. *Id.*, Einführung in die Vererbungslehre, 3. Aufl., Leipzig. On the whole subject cf. also Ztschr. f. induktive Abstammungs- und Vererbungslehre, Berlin. *Id.*, Einführung in die Vererbungswissenschaft, 3. Aufl., Berlin 1920. Tischler, Allgemeine Pflanzenkaryologie, 1922. Winkler, Ber. 3. Jahresvers. d. deutsch. Ges. f. Vererbung, Leipzig 1924. Wilson, The Cell in Development and Heredity, 3rd Ed., New York 1925. Johannsen, Elemente der exakten Erblichkeitslehre, Jena 1926. Harder, Ztschr. f. Bot., vol. 19, 1927. Oehlkers, Erblichkeitsforschung an Pflanzen, 1927.

115. Kölreuter, Vorl. Nachr. von einigen das Geschlecht der Pflanzen betreffenden Versuchen und Beobachtungen (Ostwalds Klassiker Nr. 41), 1761–66. Focke, Die Pflanzenmischlinge, Berlin 1881. de Vries, Die Mutationstheorie, 1904. Baur, Naturwissenschaften, vol. 15, 1927.

116. Mendel, reprinted in Flora, vol. 89, and Ostwalds Klassiker, Nr. 121, 1866. de Vries, Ber. d. deutsch. bot. Ges., vol. 18, 1900. *Id.*, Die Mutationstheorie, Leipzig 1903. Correns, Ber. d. deutsch. bot. Ges., vol. 18, 1900. Tschermak, Ztschr. f. landw. Versuchswesen in Österreich, 1900. Correns, Sitzungsber. Akad. Berlin 1918.

117. Correns, Bestimmung u. Vererbung des Geschlechts, Berlin 1907. *Id.*, Naturwissenschaften, 1918. *Id.*, Ber. Berliner Akad. u. Hereditas, 1921. Wettstein, Naturwissenschaften, 1923. Blackburn, Nature, Nov., vol. 10, 1923. Schaffner, Am. Nat., vol. 59, 1925. Correns, Ztschr. f. ind. Abst. u. Vererbungslehre, vol. 41, 1926.

118. Baur, cited in **93**, 1919. Lehmann, Ztschr. f. ind. Abst., vol. 13, 1914. Renner, Ztschr. f. ind. Abst., vol. 27, 1922. Baur, Bibliotheca genetica, vol. 4, 1924. Renner, Ztschr. f. ind. Abst., vol. 33, 1924.

119. Morgan, Die stoffliche Grundlage der Vererbung. Deutsch von Nachtsheim, Berlin 1922. Seiler, Ztschr. f. ind. Abst., vol. 27, 1922.

120. Seiler, Naturwissenschaften, vol. 12, 1924.

121. Darwin, The Variation of Animals and Plants under Domestication. de Vries, 1903, see **95**. Baur, Einf. in die Abstammungslehre, 3. Aufl., Berlin 1919. Winkler, Ztschr. f. ind. Abst., vol. 27, 1922. Turesson, Hereditas, vol. 3,

1922. *Id.*, Hereditas, vol. 6, 1925. Johannsen, Elemente der exakten Erblichkeitslehre, Jena 1926. Philiptschenko, Variabilität u. Variation, Berlin 1927.

122. de Vries, 1903, cited in 95. *Id.*, Die Mutation in der Erblichkeitslehre, Berlin 1912. Korschinsky, Flora, vol. 89, 1906. Renner, Ztschr. f. ind. Abst., vol. 18, 1917; Naturwissenschaften 1918. Baur, Ztschr. f. ind. Abst., vol. 18, 1918. *Id.*, Bibliotheca genetica, vol. 4, 1924.

122*a*. Lehmann, Die Theorien der Oenotheraforschung, Jena 1922. Schull, Eugenics, Genetics and the Family, vol. 1 1923. Renner, Bibliotheca genetica, vol. 9, 1925.

123. Darwin, Origin of Species. Lamarck, Philosophie zoologique, 1809. Lotsy, Vorlesungen über Deszendenztheorie, Jena 1908. Tammes, Ztschr. f. ind. Abst., vol. 36, 1925. Baur, *ib.*. vol. 37 1925.

MOVEMENT

Movements of Locomotion.

124. Pringsheim, Reizbewegungen d. Pflanzen, Berlin 1912. Jost, Reizbewegungen in Handw. d. Naturwiss., vol. 8, Jena 1913.

125. Ulehla, Biol. Zentralbl., vol. 31, 1911. Buder, Jahrb. f. wiss. Bot., vol. 56, 1915. Metzner, Jahrb. f. wiss. Bot., vol. 59, 1920; Biol. Zentralbl., vol. 40. Metzner, Beitr. z. allgem. Bot., vol. 2, 1922. *Id.*, Naturwissenschaften, vol. 11, 1923.

126. Müller, Ber. d. deutsch. bot. Ges., vol. 27, 1908.

127. Schmid, Jahrb. f. wiss. Bot., vol. 62, 1913. Ullrich, Planta, vol. 2, 1926.

127*a*. Seifriz, New Phytologist, vol. 21, 1922. Fitting, Jahrb. f. wiss. Bot., vol. 68, 1928.

128. Rothert, Flora, vol. 88, 1901. Jennings, Das Verhalten der niederen Organismen, Leipzig 1910. Buder, Jahrb. f. wiss. Bot., vol. 56, 1915; vol. 58, 1917. Oltmanns, Ztschr. f. Bot., vol. 9, 1917.

129. Senn, Die Gestalts- u. Lageveränderungen der Pflanzenchromatophoren, Leipzig 1908. *Id.*, Ztschr. f. Bot., vol. 11, 1919.

130. Pfeffer, Unters. Bot. Inst. Tübingen, vol. 1, 1884. Rothert, Flora, vol. 88, 1901. Kniep, Jahrb. f. wiss. Bot., vol. 43, 1906. Shibata, Jahrb. f. wiss. Bot., vol. 49, 1911. Kusano, Journ. Coll. of Agric. Tokyo, vol. 2, 1909.

130*a*. Köhler, Arch. f. Protistenk., 1922. Metzner, Ber. d. deutsch. bot. Ges., vol. 42, 1924. Reimers, Jahrb. f. wiss. Bot., vol. 67, 1927. Keferstein, Bot. Arch., vol. 20, 1927.

Movements of Curvature.

131. Steinbrinck, Biol. Zentralbl., vol. 26, 1906. Höber, Physik. Chemie der Zelle u der Gewebe, 6. Aufl., 1926.

132. Steinbrinck, Teubners "Monatshefte," vol. 11, 1918. Renner, Jahrb. f. wiss. Bot., vol. 56, 1915. Ursprung, Ber. d. deutsch. bot. Ges., vol. 33, 1915. Overbeck, Jahrb. f. wiss. Bot., vol. 63, 1924. *Id.*, Ber. d. deutsch. bot. Ges., vol. 43, 1925. *Id.*, Naturwissenschaften, vol. 14, 1926.

133. Goebel, Entfaltungsbewegungen, 2. Aufl., Jena 1924. Priestley, New Phytologist, vol. 24, 1925; vol. 25, 1926. Linsbauer, Planta, vol. 1, 1926. Gradmann, Naturwissenschaften, vol. 15, 1927.

134. Pfeffer, Die Reizbarkeit der Pflanzen (Verhandl. d. Ges. d. Naturforscher), 1893. Noll, Sinnesleben der Pflanze (Ber. Senckenberg. Gesellsch.), 1896. Fitting, Reizleitung (Ergebn. d. Physiologie, vols. 4-5), and Jahrb. f. wiss. Bot., vols. 44-45, 1905–07. Jost, Reizbewegungen in Handw. d. Naturw., vol. 8, Jena 1923.

Tropisms.

135. Knight, Ostwalds Klassiker, vol. 62, 1806. Fitting, Jahrb. f. wiss. Bot., vol. 41, 1905. *Id.*, Handw. d. Naturw., Reizbewegungen, vol. 8, Jena 1913. Giltay, Ztschr. f. Bot., vol. 2, 1910. Zimmermann, Erg. d. Biologie, 1927.

136. Engler, A., Tropismen u. exzentrisches Dickenwachstum, Zürich 1918. Jost, Bot. Ztg., vol. 59, 1901. Riss, Ztschr. f. Bot., vol. 7, 1915. Jost, Ber. d.

deutsch. bot. Ges., vol. 42, 1924. Bremecamp, Ber. d. deutsch. bot. Ges., vol. 43, 1925.

137. Zollikofer, Rec. trav. bot. néerl., vol. 18, 1922. Koningsberger, *Ib.*, 1922. Renner, Ztschr. f. Bot., vol. 14, 1922. v. Ubisch, Jahrb. f. wiss. Bot., vol. 64, 1924. Jost and Wissmann, Ztschr. f. Bot., vol. 16, 1924. Zimmermann, Jahrb. f. wiss. Bot., vol. 63, 1924. *Id.*, Jahrb. f. wiss. Bot., vol. 66, 1927.

137*a*. André, Ber. d. deutsch. bot. Ges., vol. 45, 1927. Zimmermann, Naturwissenschaften, vol. 15, 1927.

138. Noll, Heterogene Induktion, Leipzig 1892. *Id.*, Sitzungsber. niederrhein. Ges., 1901. Nienburg, Flora, vol. 102, 1911. Bremekamp, Rec. trav. bot. néerl., vol. 9, 1912. Rawitscher, Ber. d. deutsch. bot. Ges., vol. 44, 1926. Gradmann, Naturwissenschaften, vol. 15, 1927.

139. Oehlkers, Jahrb. f. wiss. Bot., vol. 61, 1922. Schmitt, Ztschr. f. Bot., vol. 14, 1922. Schwieke, Ausz. Diss. Hamburg, 1922. Boas and Merkenschlager, Ber. d. deutsch. bot. Ges., vol. 43, 1925. Sperlich, Planta, vol. 2, 1926.

140. Zollikofer, Beitr. z. allgem. Bot., vol. 1, 1918. Stahl, Flora, vol. 111, 1919. Noll, Heterogene Induktion, Leipzig 1892. Nemec, Ber. d. deutsch. bot. Ges., vol. 18, 1900; further, Jahrb. f. wiss. Bot., vol. 36. *Id.*, Studien über Regeneration, Berlin 1905. Haberlandt, Ber. d. deutsch. bot. Ges., vol. 18, 1900; further, Jahrb. f. wiss. Bot., vols. 38, 42, 44. Zollikofer, Rec. trav. bot. néerl., vol. 18, 1922. Zaepfel, Ann. sc. nat., vol. 5, 1923. Zimmermann, Ber. d. deutsch. bot. Ges., vol. 42, 1924. Rawitscher, Ztschr. f. Bot., vol. 17, 1925. Lundegardh, Planta, vol. 2, 1926. Weber, Jahrb. f. wiss. Bot., vol. 66, 1927.

141. Stoppel, Jahrb. f. wiss. Bot., vol. 62, 1923. Cholodny, Beih. bot. Zentralbl., 1923. *Id.*, Jahrb. f. wiss. Bot., vol. 65, 1926. Brauner, Jahrb. f. wiss. Bot., vol. 66, 1927.

142. Rutten-Pekelharing, Trav. bot. néerl., vol. 7, 1910. Tröndle, Jahrb. f. wiss. Bot., vol. 52, 1913. *Id.*, N. Denkschr. schweiz. nat. Ges., vol. 51, 1915. *Id.*, Jahrb. f. wiss. Bot., vol. 60, 1921.

143. Wiesner, Heliotrop. Erscheinungen (Denkschriften k. k. Akad. Wien), 1878–80. Stahl, Kompaßpflanzen, Jena 1881. Oltmanns, Flora, vol. 75, 1892; vol. 38, 1897. E. Pringsheim, Beitr. z. Biol., vol. 9, 1907–9. Arisz, Kon. Akad. Amsterdam. Proceed. 1911. Rothert, Cohns Beitr. z. Biol., vol. 7, 1896. Brauner, Ergebn. d. Biol., 1927.

144. Blaauw, Med. van Landbouwhoogeschool Wageningen, vol. 15, 1918. Sierp, Ztschr. f. Bot., vol. 11, 1919; Ber. d. deutsch. bot. Ges., vol. 37. Sande Bakhuyzen, Analyse der fototrop. Stemmingsverschijnselen Groningen, 1920. Brauner, Ztschr. f. Bot., vol. 14, 1922. Lundegårdh, Arkiv för Bot., vol. 18, 1922. Pisek, Jahrb. f. wiss. Bot., vol. 65, 1926. Brauner, Ergebn. d. Biologie, vol. 2, Berlin 1927. Nuernbergk, Bot. Abhandl., 12 H. 1927. Beyer, Planta, vol. 4, 1927. Went, Rec. trav. bot. néerl., vol. 25, 1928. Pisek, Jahrb. f. wiss. Bot., vol. 67, 1928.

145. Engler, A., 1918, cited in **91**.

146. Haberlandt, Sitzungsber. Akad. Berlin 1916. Nordhausen, Ztschr. f. Bot., vol. 9, 1917. Buder, Ber. d. deutsch. bot. Ges., vol. 38, 1920. *Id.*, Jahrb. f. wiss. Bot., vol. 58, 1917. Lundegårdh, 1922, see **119**. v. Guttenberg, Beitr. z. allgem. Bot., vol. 2, 1922. Nuernbergk, Bot. Abhandl., 12 H. 1927.

147. Denecke, Mitt. Inst. f. allgem. Bot. Hamburg, vol. 6, 1924. Nuernbergk. Bot. Abhandl., 8 H. 1925. Meylau, Mem. soc. Vand. sc. nat., vol. 2, 1925. Raydt, Jahrb. f. wiss. Bot., vol. 64, 1925. Stocker, Flora, vol. 20, 1926.

148. Oltmanns, Flora, vol. 83, 1897. Pringsheim, Beitr. z. Biol., vol. 9, 1907; vol. 10, 1908. Arisz, Rec. des. trav. bot. néerl., vol. 12, 1915. Blaauw, Rec. trav. bot. néerl., vol. 5, 1909. Sande Bakhuyzen, 1920, see **145**. Oehlkers, 1922, see **115**. Koningsberger, Rec. trav. bot. néerl., vol. 20, 1923.

149. Darwin, Power of Movement in Plants. Voechting, Bot. Ztg., vol. 46, 1888. Rothert, Cohns Beitr. z. Biol., vol. 7, 1896. Haberlandt, Lichtsinnesorgane L., 1905. Fitting, Jahrb. f. wiss. Bot., vols. 44-45, 1907. Kniep, Biol. Zentralblatt., vol. 27, 1907. Nordhausen, Ber. d. deutsch. bot. Ges., vol. 25, 1907. Blaauw, Rec. trav. bot. néerl., vol. 5, 1909. van der Wolk, Proc. Akad., Amsterdam 1911. Buder, Jahrb. f. wiss. Bot., vol. 58, 1917. Stark, Jahrb. f. wiss. Bot., vol. 61, 1922. Burckhardt, Ztschr. f. Bot., vol. 18, 1926.

150. Nathansohn and Pringsheim, Jahrb. f. wiss. Bot., vol. 45, 1908.

151. Fitting, Jahrb. f. wiss. Bot., vol. 44, 1907. Boysen-Jensen, Ber. d. deutsch. bot. Ges., vol. 31, 1911. Paal, Jahrb. f. wiss. Bot., vol. 58, 1918. Sierp and Seybold, Jahrb. f. wiss. Bot., vol. 65, 1926. Lange, Jahrb. f. wiss. Bot., vol. 67, 1927. Stark, Erg. d. Biol., vol. 2, 1827.

152. Brauner, Ztschr. f. Bot., vol. 16, 1924. Went, Rec. trav. bot. néerl., vol. 25, 1928.

153. Molisch, Sitzungsber. Wiener Akad., vol. 88, 1883. *Id.*, Sitzungsber. Wiener Akad., vol. 90, 1884. Porodko, Ber. d. deutsch. bot. Ges., vol. 30, 1912. Hooker, Annals of bot., vol. 29, 1915. Polowzow, Unters. über Reizersch., Jena 1909. Walter, Ztschr. f. Bot., vol. 13, 1921. Müller, Beitr. z. allgem. Bot., vol. 2, 1922.

154. Stark, Jahrb. f. wiss. Bot., vol. 57, 1917. *Id.*, *ibid.*, vol. 60, 1921. Beyer, Biol. Zentralbl., vol. 45, 1925. Bünning, Bot. Arch., vol. 16, 1926. *Id.*, Ztschr. f. Bot., vol. 19, 1927.

155. Darwin, Climbing Plants. Pfeffer, Unters. bot. Inst. Tübingen, vol. 1, 1885. Fitting, Jahrb. f. wiss. Bot., vol. 38, 1903. Schenck, Beitr. z. Biol. d. Lianen, Jena 1892. Peirce, Annals of bot., vol. 8, 1894. Goebel, 1920, cf. **132.** Stark, Jahrb. f. wiss. Bot., vol. 61, 1922.

156. Stark, Jahrb. f. wiss. Bot., vol. 57, 1916; Ber. d. deutsch. bot. Ges., vol. 35, 1917. *Id.*, Handb. norm. u. path. Physiol XI. Haptotropismus, Seismonastie, Traumatropismus bei Pflanzen, 1926.

157. Stark, Jahrb. f. wiss. Bot., vol. 58, 1918.

158. Gassner, Ber. d. deutsch. bot. Ges., vol. 41, 1923. Treitel, Bot. Arch., vol. 7, 1924. Zeidler, Bot. Arch., vol. 10, 1925. Silberschmidt, Ber. d. deutsch. bot. Ges. vol. 43, 1925. Erman, *ibid.*, vol. 44, 1926. Sierp, *ibid.*, vol. 44, 1926.

159. Voechting, Bewegungen der Blüten u. Früchte, Bonn 1882. Simon, Jahrb. f. wiss. Bot., vol. 51, 1912. Harder, Ber. d. deutsch. bot. Ges., vol. 32, 1914. Sierp, Ztschr. f. Bot., vol. 10, 1918. Pisek, Jahrb. f. wiss. Bot., vol. 65, 1926.

Nastic Movements.

160. Kniep, Handw. d. Naturwiss., vol. 8, Jena 1913: Reizerscheinungen. Linsbauer, Flora, vol. 109, 1916. Iljin, Biochem. Ztschr., vol. 132, 1922. Steinberger, Biol. Zentralbl., vol. 42, 1922. Goebel, Die Entfaltungsbewegungen, Jena 1924.

161. Iljin, Biochem. Ztschr., vol. 132, 1922.

162. Pfeffer, Periodische Bewegungen, Leipzig 1875. *Id.*, Unters. über Entstehung der Schlafbewegungen (Abh. K. Ges. d. Wiss., Leipzig), 1907. Stoppel, Ztschr. f. Bot., vol. 2, 1910. Stoppel and Kniep, *ibid.*, vol. 3, 1911. Brauner, Jahrb. f. wiss. Bot., vol. 65, 1926. Fhese, Planta, vol. 3, 1927.

163. Nuernbergk, Bot. Abh., 8 Heft, 1925. Meylau, Mem. soc. Vand. sc. nat., vol. 2, 1925.

164. Pfeffer, Abh. K. Ges. Leipzig, vol. 34, 1915. Stoppel, Ztschr. f. Bot., vol. 8, 1916. *Id.*, *ibid.*, vol. 12, 1920. Sperlich and Schweidler, Ztschr. f. Bot., vol. 14, 1922. Cremer, Ztschr. f. Bot., vol. 15, 1923. Stoppel, Planta, vol. 2, 1926. Brouwer, De periodieke Bewegingen van de primaire Bladeren bij Canavalia eusiformis, Diss. Utrecht 1926. Walde, Jahrb. f. wiss. Bot., vol. 66, 1927.

165. Darwin, Insectivorous Plants. Hooker, Bull. Torrey Club, vol. 43, 1916.

166. Brücke, Archiv f. Anat. u. Physiol. (Ostwalds Klassiker, vol. 95, 1848). Bert, Mém. Soc. Bordeaux, Paris 1867-70. Pfeffer, Physiologische Untersuchungen, 1873.

167. Haberlandt, Sinnesorgane im Pflanzenreich, Leipzig 1901. Fitting, Ergebn. d. Physiol., vol. 4, 1905; vol. 5, 1906. Bose, Res. on irritability of plants, Bombay and Calcutta 1913. Ricca, Nuovo giornale bot. ital., vol. 23, 1926; Arch. ital. de biol., vol. 65. Linsbauer, Ber. d. deutsch. bot. Ges., vol. 32, 1914. Goebel, 1920, cf. **160.** Linsbauer, Jahrb. f. wiss. Bot., vol. 62, 1923. Snow,

Proc. Roy. Soc. London, Ser. B., vol. 96, 1924. *Id.*, Ann. of Bot., vol. 38, 1924. Umrath, Sitzungsber. Ak. Wiss. Wien, vol. 134, 1925. *Id.*, Planta, vol. 5, 1928.

168. Stark, see **155**, **156**, **157**. von Guttenberg, Flora, vols. 118-119, 1925.

THALLOPHYTA, BRYOPHYTA, PTERIDOPHYTA,

BY R. HARDER

1. Engler-Prantl, Natürl. Pflanzenfamilien, vol. 1. Lotsy, Vorträge über Bot. Stammesgeschichte, vol. 1, 1907; vol. 2, 1909. L. Rabenhorsts Kryptogamenflora von Deutschland, Österreich und der Schweiz. Pascher, Die Süßwasserflora Deutschlands, Österreichs und der Schweiz. H. Kniep, Die Sexualität der niederen Pflanzen 1928.

2. Klebs, Die Bedingungen der Fortpflanzung bei niederen Algen und Pilzen 1896 and Jahrb. f. wiss. Bot., vols. 32-34. *Id.*, Willkürl. Entwicklungsänd. bei Pflanzen 1903.

Lower Thallophyta.

3. A. Fischer, Vorlesung. über Bakterien 1897, 2. Aufl. 1903. Miehe, Bakterien, Leipzig, 2. Aufl. 1918. Lehmann and Neumann, Bakteriologie. Günther, Bakteriologie. Heim, Lehrb. d. Bakt. Löhnis, Landw.-bakt. Praktikum 1911. Benecke, Bau u. Leben der Bakterien 1912. A. Meyer, Die Zelle der Bakterien 1912. Viehöver, Ber. d. deutsch. bot. Ges., vol. 30, 1912, p. 443. R. Lieske, Bakterienkunde 1926. F. Fuhrmann, Einführung in die technische Mykologie 1926. H. Ullrich, Planta, vol. 2, 1926, p. 295.

3*a*. Buder (Thiospirillum), Jahrb. f. wiss. Bot., vol. 56, 1915, p. 525. Metzner, Biol. Zentralbl., vol. 40, 1920, p. 49; and Jahrb. f. wiss. Bot., vol. 59, 1920, p. 325.

3*b*. H. Potthoff, Zentralbl. f. Bakt. II, vol. 61, 1924, p. 249.

4. Molisch, Die Purpurbakterien, Jena 1907. Buder, Jahrb. f. wiss. Bot., vol. 58, 1919, p. 525.

5. Molisch, Leuchtende Pflanzen, 2. Aufl. 1912. G. Meissner, Zentralbl. f. Bakt. II, vol. 67, 1926, p. 194.

6. D'Hérelle, Der Bakteriophag. 1922. H. v. Preiss, Die Bakteriophagie 1925. Koch, Bot. Archiv, vol. 19, 1927, p. 275.

6*a*. Barthel, Ztschr. f. Gärungsphysiol. 1917, p. 13.

7. Sorauer, Graebner, Lindau, Reh, Handb. d. Pflanzenkrankh., 4. Aufl. 1921. W. Magnus, Ber. d. deutsch. bot. Ges., vol. 33, 1915, p. 96. Smith, Bacterial Diseases of Plants, 1920. C. Stapp, Ber. d. deutsch. bot. Ges., vol. 55, 1927, p. 55. A. Brusoff, Zentralbl. f. Bakt. II, vol. 63, p. 256. Link and Sharp, Bot. Gazette, vol. 83, 1917, p. 145.

8. Miehe, Ztschr. f. Hyg. u. Infekt., vol. 62, 1908, p. 155. R. Lieske, Bakterien und Strahlenpilze, Handb. d. Pflanzenanat., II, Abt., 1. Teil, 1922.

9. Keil, Schwefelbakterien, Diss. Halle a. S. 1912. Düggeli, Nat. Wochenschr. 1917, p. 321. Bavendamm, Pflanzenforschung, H. 2. 1924.

9*a*. Molisch, Die Eisenbakterien 1910. Lieske, Jahrb. f. wiss. Bot., vol. 49, 1911, p. 91. N. Cholodny, Die Eisenbakterien 1926.

9*b*. G. Schmidt, Arch. f. Hyg., vol. 91, p. 339.

9*c*. B. Schussnig, Verh. zool. bot. Ges. Wien, vol. 75, 1925, p. 196. Guillermond, Compt. rend. soc. biol., vol. 34, 1926, p. 579. Geitler, Arch. f. Protistenk., vol. 50, 1924, pp. 67, 511. E. Jahn, Die Polyangiden 1924.

10. A. Fischer, Unters. über den Bau der Cyanophyceen u. Bakterien 1897; further, Bot. Ztg. 1905, p. 51. Hegler, Jahrb. f. wiss. Bot., vol. 36, 1901, p. 229. Massart, Recueil de l'inst. bot. de Bruxelles, vol. 5, 1902. Brand, Ber. d. deutsch. bot. Ges. 1901, p. 152; 1905, p. 62, and Beih. Bot. Zentralbl., vol. 15, 1903, p. 31. Fritsch, Beih. Bot. Zentralbl., vol. 18, 1905, p. 194. Olive, Beih. Bot. Zentralbl., vol. 18, 1905, p. 9. Guillermond, Revue génér. de bot., vol. 18, 1906, p. 392. E. Pringsheim, Die Naturwissenschaften 1913, p. 495. Fechner, Ztschr. f. Bot., vol. 7, 1915, p. 289. Pieper, Diss. Berlin 1915. Klein, Anzeig. Akad. Wien, vol. 52, 1915. Boresch, Archiv f. Protist., vol. 44, 1921, p. 1, and Biochem.

Ztschr., vol. 119, 1921, p 167. BAUMGÄRTEL, Archiv f. Protist., vol. 43, 1920, p. 50. GEITLER, Sitzber. Wiener Akad., math.-nat. Kl. 1921, p. 223. *Id.*, Arch. f. Protist., vol. 45, 1922, p. 413 ; Beih. Bot. Zentralbl., II. Abt., vol. 41, 1925, p. 63. Die Cyanophyceen (in PASCHERS Süsswasserflora 1925). A. W. HAUPT, Bot. Gazette 1923. HARDER, R., Ztschr. f. Bot., 1923. S. PRATT, Arch. f. Protist., vol. 52, 1925, p. 142. GUILLERMOND, A. Rev. gén. bot., vol. 38, 1926, p. 129.

10*a*. G. SCHMID, Flora, N. F., vol. 11, 1918, p. 327. R. HARDER, Ztschr. f. Bot., vol. 10, 1918, p. 177 ; vol. 12, 1920, p 353. G. SCHMID, Jahrb. f. wiss. Bot., vol. 60, 1921, p. 572 ; *ibid.*, vol. 62, 1923, p. 328.

10*b*. R. HARDER, Ztschr. f. Bot., vol. 9, 1917, p. 145. A. LIMBERGER, Sitzber. Wiener Akad., math.-nat. Kl., Abt. 1, vol. 134, 1925, p. 1. H. MOLISCH, Sci. rep. Tohoku Univ. Ser. IV Biol., vol. 1, p. 169.

11. OLTMANNS, Morphologie u. Biologie der Algen, 2. Aufl. 1922.

12. SENN, Ztschr. f. wiss. Zool., vol. 97, 1911, p. 605. F. DOFLEIN, Lehrb. d. Protozoenkunde, 4. Aufl. 1916. PASCHER, Ber. d deutsch. bot. Ges., vol. 29, 1911, p. 193 ; vol. 32, 1914, p. 136 ; vol. 34, 1916, p. 440, and Archiv f. Protistenk., vol. 25, 1912, p. 153 ; vol. 36, 1915, p. 81. PASCHER, Flagellaten u. Rhizopoden in ihren gegenseitigen Beziehungen 1917, and Ber. d. deutsch. bot. Ges. 1921, p. 236. DOFLEIN, Arch. f. Protistenk., vol. 44, 1922, p. 149 ; vol. 46, 1923, p. 267. A. SCHERFFEL, Arch. f. Protistenk., vol. 48, 1924, p. 187. A. KORSHIKOV, Arch. f. Protistenk., vol. 58, 1927, p. 441. PASCHER, Ber. d. deutsch. bot. Ges., vol. 42, 1924, p. 148 ; Arch. f. Protistenk., vol. 51, 1925, p. 556 ; vol. 58, 1927, p. 1.

12*a*. LEMMERMANN, Ber. d. deutsch. bot. Ges., vol. 19, 1901, p. 247.

12*b*. LOHMANN, Archiv f. Protistenk., vol. 1, 1902, p 89. SCHILLER, Die Naturwissenschaften, vol. 4, 1916, p. 277. SJÖSTEDT, Lunds Univ. Arsskr., vol. 20, N. F. Avd. 2, 1924.

12*c*. CH. TERNETZ, Jahrb. f. wiss. Bot., vol. 51, 1912, p. 435. SKORTZOW, Arch. f. Protistenk., vol. 48, 1924, p. 180. MAINX, *ibid.*, vol. 60, 1928, p. 305.

12*d*. M. HARTMANN, Die Konstitution der Protistenkerne 1911. BELAR, Ergebn. u. Fortschr. d. Zool., vol. 6, 1926, p. 235. REICHARDT, Arch. f. Protistenk., vol. 59, 1927, p. 301.

12*e*. A. PASCHER, Arch. f. Protistenk., vol. 52, 1925, p. 489 ; vol. 58, 1927, p. 35 ; Ber. d. deutsch. bot. Ges., vol. 44, 1926, p. 394. POULTON, Bull. soc. bot. Genève, 2. Sér., vol. 17, 1925, p. 33. R. KOLKWITZ, Ber. d. deutsch. bot. Ges., vol. 44, 1926, p. 533. V. MILLER, *ibid.*, vol. 45, 1927, p. 151.

13. A. LISTER, Monograph of the Mycetozoa, ed. 2. HARPER, Bot. Gaz., vol. 30, 1900, p. 217. PAVILLARD, Progressus rei bot., vol. 3, 1910, p. 496. PASCHER, Ber. d. deutsch. bot. Ges., vol. 36, 1918, p. 359.

14. JAHN, Ber. d. deutsch. bot. Ges., 1911, p. 231. *Id.*, Ber. d. deutsch. bot. Ges., vol. 46, 1928, p. 8. WILSON, MALCOLM, and CADMAN, Journ. Sci. Transact. Brit. Ass. Adv. of Sci. Oxford, 1926, p. 73.

15. WORONIN, Jahrb. f. wiss. Bot., vol. 11, 1878, p. 548. NAWASCHIN, Flora, 1899, p. 404. PROWAZEK, Arb. kaiserl. Gesundheitsamt, vol. 22, 1905, p. 396. MARCHAND, Compt. rend. Acad. Paris, vol. 150, 1910, p. 1348. SCHWARTZ, Annals of bot., vol. 25, 1911, p. 791, and vol. 28, 1914, p. 227. JAHN, Ztschr. f. Bot., vol. 6, 1914, p. 875.

16. THAXTER, Bot. Gaz., vol. 14, 1892, p. 389 ; vol. 23, 1897, p. 395 ; and vol. 37, 1904, p. 405. QUEHL, Zentralbl. f. Bakt., etc., vol. 2, 1906, p. 9. VAHLE, *ibid.*, vol. 25, 1909, p. 178. JAHN, Ber. d. deutsch. bot. Ges., vol. 36, 1918, p. 4. *Id.*, Die Polyangiden, 1924.

17. SCHÜTT, Die Peridin. der Planktonexpedition 1895. SCHILLING, Flora, 1891, p. 220, and Ber. d. deutsch. bot. Ges. 1891, p. 199. JOERGENSEN, Die Ceratien, Leipzig 1911. KLEBS, Verh. nat. med. Verein Heidelberg, vol. 9, 1912, p. 369. SCHILLING, Die Dinoflagellaten in PASCHER's Süsswasserflora Deutschlands 1913. KOFOID and SWEZY, Mem. univ. Californ., vol. 5, 1921. ENTZ, Arch. f. Protistenk., vol. 56, 1926, p. 395. N. PETERS, Zool. Anz., vol. 73, 1927, p. 143.

18. SCHÜTT, Das Pflanzenleben der Hochsee 1893. GRAN, Das Plankton des norwegischen Nordmeeres 1902. G. KARSTEN, Wiss. Ergebn. d. deutsch. Tiefsee-Expedition 1898–99, vol. 2, 2. Teil, 1905–1907. BENNIN, Arch. f. Hydrobiol., vol. 16, 1925, p. 340.

19. HUBER and NIPKOW, Flora, vol. 116, 1923, p. 114.

20. Dippel, Diatomeen der Rhein-Mainebene 1905. von Schönfeldt, Diatomaceae Germaniae 1907. O. Müller, Ber. d. deutsch. bot. Ges. 1898–1909. Heinzerling, Bibl. bot. Heft 69, 1908. Mangin, Ann. sc. nat. 9. Sér., vol. 8, 1908, p. 177. G. Karsten, Handw. d. Naturw., vol. 2, p. 960. *Id.*, Ztschr. f. Bot., vol. 4, 1912, p. 417. Funk, Ber. d. deutsch. bot. Ges., vol. 37, 1919, p. 190. Beger, Ber. d. deutsch. bot. Ges., vol. 45, 1927, p. 385. Liebsch, Ztschr. f. Bot., vol. 20, 1928, p. 3.

21. Gran, Die Diat. der arkt. Meere, Fauna arctica, vol. 3, 1904. G. Karsten, Ber. d. deutsch. bot. Ges. 1904, p. 544, and Wiss. Ergebn. d. deutsch. Tiefsee-Expedition, vol. 2, 2. Teil, 1907, p. 496. P. Bergon, Bull. Soc. bot. France, vol. 54, 1907, p. 327. Pavillard, Bull. Soc. bot. France, vol. 61, 1914, p. 164. Schiller, Ber. d. deutsch. bot. Ges., vol. 27, 1909, p. 351. P. Schmidt, cf. Oltmanns, Algen, 2. Aufl. I, p. 193. Ikari, Bot. Mag. Tokyo, vol. 37, 1923. G. Karsten, Intern. Rev. ges. Hydrobiol., vol. 12, 1924, p. 116; vol. 13, 1925, p. 326. P. Schmidt, Intern. Rev. d. ges. Hydrobiol., vol. 11, 1923, p. 114; vol. 17, 1927, pp. 274, 400. Gemeinhardt, Pflanzenforschungen, 6. H. 1926. Geitler, Biol. Zentralbl., vol. 47, 1927, p. 403.

22. Benecke, Jahrb. f. wiss. Bot., vol. 35, 1900, p. 535. G. Karsten, Flora, Ergzb. 1901, p. 404. Richter, Denkschr. Akad. Wien, vol. 84, 1909.

23. Schussnig, Zool. bot. Ges. Wien, 1925, p. 224; Nuova Notarisia, 1925, p. 319. Steinecke, Bot. Arch., vol. 13, 1926, H. 3-4.

24. W. West and G. S. West, A Monograph of the Brit. Desmid., vol. 1, 1904. Kauffmann, Ztschr. f. Bot., 1914, p. 721.

24*a*. Wehrle, Ztschr. f. Bot., vol. 19, 1927.

25. Lutman, Bot. Gaz., vol. 49, 1910, p. 241; vol. 51, 1911, p. 401. van Wisselingh, Ztschr. f. Bot., vol. 4, 1912, p. 337. Potthoff, Planta, vol. 4, 1927, p. 261.

26. Tröndle, Ztschr. f. Bot., vol. 3, 1911, p. 593, and vol. 4, 1921, p. 721. Kurssanow, Flora, vol. 104, 1911, p. 65. Hemleben, Bot. Arch., vol. 2, 1922, p. 149. Czurda, Arch. f. Protistenk., vol. 51, 1925, p. 438. Benecke, Flora, vol. 119, 1925, p. 27.

Algae.

27. Pascher, Hedwigia, vol. 53, p. 6.

28. Kützing, Tabulae phycologicae. Mast, Arch. f. Protistenk., vol. 60, 1928, p. 197.

28*a*. Brand, Arch. f. Protistenk., vol. 52, 1925, p. 265. G. Schmidt, Ber. d. deutsch. bot. Ges., vol. 45, 1927, p. 518.

29*a*. Wollenweber, Ber. d. deutsch. bot. Ges., vol. 26, 1908, p. 238.

29*b*. Goroschankin, Flora 1905, p. 420.

30. Zimmermann, Jahrb. f. wiss. Bot., vol. 60, 1921, p. 256. M. Hartmann, Arch. f. Protistenk., vol. 49, 1924, p. 375. Uspenski, Ztschr. f. Bot., vol. 17, 1925, p. 273. Schreiber, *ibid.*, p. 337. Bock, Arch. f. Protistenk., vol. 56, 1926, p. 321. B. Schulze, *ibid.*, vol. 59, 1927, p. 508.

31. Gerneck, Beih. Bot. Zentralbl., vol. 21^2, p. 221. Treboux, Ber. d. deutsch. bot. Ges., vol. 30, 1912, p. 69.

32. Grintzesco, Rev. génér. de bot., vol. 15, 1903, p. 5. Goetsch and Scheuring, Ztschr. f. Morph. u. Ökol. d. Tiere, vol. 7, 1926, p. 320. W. Vischer, Bull. soc. bot. Genève, vol. 18, 1926, p. 22.

33. Harper, Bull. Univ. Wisconsin, No. 207, 1908, p. 280.

33*a*. Carter, Ann. of Bot., vol. 40, 1926, p. 665.

34. Pascher, Hedwigia, vol. 46, 1907, p. 265. van Wisselingh, Beih. Bot. Zentralbl., vol. 23, I, 1908.

35. Allen, Ber. d. deutsch. bot. Ges. 1905, p. 285.

36. Haberlandt, Sitzber. Akad. Wien, vol. 115, I, 1906, p. 1. Svedelius, Ceylon marine biolog. reports, No. 4, 1906.

37. Freund, Beih. Bot. Zentralbl., vol. 21, 1907, I, p. 55.

37*a*. Jollos, Biol. Zentralbl., vol. 46, 1926, p. 279.

38. Davis, Bot. Gaz., vol. 38, 1904, p. 81. Heidinger, Ber. d. deutsch. bot. Ges., vol. 26, 1908, p. 312.

38*a*. Kolkwitz and Kolbe, Ber. d. deutsch. bot. Ges., vol. 41, 1923, p. 312.

39. Scottsberg, Wiss. Ergebn. d. schwed. Südpolarexpedition, vol. 4, 6. Lief., 1907, p. 80. Frye, Rigg, and Crandall, Bot. Gaz., vol. 60, 1915, p. 473.

41. Sauvageau, Compt. rend. Soc. de biolog. Paris, vol. 62, 1907, p. 1082. Schiller, Internat. Revue d. ges. Hydrobiol., vol. 2, 1909, p. 62. F. Borgesen, The Species of Sargassum, Kopenhagen 1914, and The marine Algæ of the Danish West Indies, Part 2, 1914, p. 222. Sjöstedt, Bot. Notiser, 1924, p. 1.

42. Hansteen, Jahrb. f. wiss. Bot., vol. 35, 1900, p. 611. Hunger, *ibid.*, vol. 38, 1903, p. 70. Kylin, Ztschr. f. Bot., vol. 4, 1912, p. 540. *Id.*, Ztschr. f. phys. Chemie, vol. 94, 1915, p. 337, and Ber. d. deutsch. bot. Ges., vol. 36, 1918, p. 10. Wille, Univers.-Festschrift Christiania 1897. Sykes, Annals of bot., vol. 22, 1908, p. 292. Kniep, Internat. Revue d. Hydrobiol., vol. 7, 1914, p. 1.

43. Yamanouchi, Bot. Gaz., vol. 48, 1909, p. 380, and Bot. Zentralbl., vol. 116, 1911, p. 435. *Id.*, Bot. Gaz., vol. 54, 1912, p. 441. Knight, Transact. R. Soc. Edinburgh, vol. 53, 1923, Part II, p. 343. Sauvageau, Compt. rend. acad. Paris, vol. 180, 1925, pp. 464, 1632.

44. M. Hartmann, Biol. Zentralbl., vol. 45, 1925, p. 449. Jollos, *ibid.*, vol. 46, 1926, p. 279.

45. Williams, Annals of bot., vol. 11, 1897, p. 545, and vol. 18, 1904, pp. 141, 183; vol. 19, 1905, p. 531. Lewis, Bot. Gaz., vol. 50, 1910, p. 59. Mottier, Annals of bot., vol. 14, 1900, p. 163. H. Heil, Ber. d. deutsch. bot. Ges., vol. 42, 1924, p. 119. Carter, Ann. of Bot., vol. 41, 1927, p. 139.

46. Sauvageau, Compt. rend Paris, vol. 161, 1915; vol. 162, 1916; vol. 163, 1917. Kylin, Svensk. bot. Tidskr., vol. 10, 1916, p. 551, and vol. 12, 1918, p. 21. Pascher, Ber. d. deutsch. bot. Ges. 1918, p. 246. Kuckuck, *ibid.*, 1917, p. 557. Williams, Annals of bot., vol. 35, 1921, p. 118. Printz, Norske Vidensk. Selsk. Skr. Trondhjem, 1922, p. 1. R. P. Brandt, U.S. Dept. of Agric. Bull. 1191, 1923

47. Yamanouchi, Bot. Gaz., vol. 47, 1909, p. 173. Nienburg, Flora, vol. 101, 1910, p. 167, and Ztschr. f. Bot., vol. 5, 1913, p. 1. Sauvageau (Cystoseira), Bull. stat. biol. d'Arcachon, 14. Jahrg. 1912. Kylin, Ber. d. deutsch. bot. Ges., vol. 38, 1920, p. 74 (Fucus-Spermatozoid). W. Kotte, Ber. d. deutsch. bot. Ges., vol. 51, 1923, p. 24.

48. Mottier, Annals of bot., vol. 18, 1904, p. 245. Strasburger, Wiesner-Festschrift 1908, p. 24. Schenck, Bot. Jahrb. f. System., vol. 42, 1908, p. 1. Oehlkers, Ber. d. deutsch. bot. Ges., vol. 34, 1916, p. 223. Goebel, Flora, N. F., vol. 10, 1918, p. 344. Ernst, Bastardierung als Ursache der Apogamie im Pflanzenreich 1918. Winkler, Verbr. u. Urs. d. Parthenogenesis, Jena 1920. K. Bessenich, Jahrb. f. wiss. Bot., vol. 62, 1923, p. 214.

49. Wolfe, Annals of bot., vol. 18, 1904, p. 607. Yamanouchi, Bot. Gaz., vol. 41, 1906, p. 425. Kurssanow, Flora, vol. 99, 1909, p. 311. Svedelius, Ber. d. deutsch. bot. Ges., vol. 32, 1914, p. 48. Schiller, Österr. bot. Ztschr. 1913, Nr. 4. v. Faber, Ztschr. f. Bot., vol. 5, 1913, p. 801. Kylin, Ber. d. deutsch. bot. Ges., vol. 35, 1917, p. 155. Cleland, Annals of bot., vol. 33, 1919, p. 323. Svedelius, Ber. d. deutsch. bot. Ges., vol. 35, 1917, p. 225. *Id.*, Kgl. Svensk. Vetenskapsakad. Handl., vol. 43, 1908, p. 76. Lewis, Annals of bot., vol. 23, 1909, p. 639, and Bot. Gaz., vol. 53, 1912, p. 236. Kuckuck, Ztschr. f. Bot., vol. 3, 1911, p. 180. Svedelius, Svensk. Bot. Tidskrift, vol. 5, 1911, p. 260, and vol. 6, 1912. p. 239. Rigg and Dalgity, Bot. Gaz., vol. 54, 1912, p. 164. Svedelius, Ber. d. deutsch bot. Ges., 1914, p. 106; Svensk. Bot. Tidskr., vol. 8, 1914, p. 1; Nova acta reg. soc. sc. Upsaliensis, Ser. 4, vol. 4, 1915. Kylin, Ber. d. deutsch. bot. Ges. 1916, p. 257; Ztschr. f. Bot. 1916, pp. 97, 545. *Id.*, Svensk. Vetensk. Akad. Handlingar, vol. 63, 1923, Nr. 11, p. 3; Lunds Univ. Arsskr., N. F., vol. 29, 1925, p. 3. Rosenvinge, Dansk. Vidensk. Selsk. Skr., vol. 7, Raekke, nat.-m. Afd. 1924, p. 284. Ishikawa, Bot. Mag. Tokyo, vol. 38, 1924, p. 159. Grubb, Journ. Linn. Soc. London, Bot., vol. 47, 1925, p. 177. Sjöstedt, Lunds Univ. Arsskr., N. F. Afd. 2, vol. 22, 1926, Nr. 4. Svedelius, Nova Acta Reg. Soc. Sci. Upsala, 1927. Schussnig and Odle, Arch. f. Protistenk., vol. 58, 1927, p. 220.

50. Kuckuck, Sitzber. Akad. Berlin 1894, p. 983. Sturch, Annals of bot., vol. 13, 1899, p. 83. Eddelbüttel, Bot. Ztg. 1910, p. 186. Sturch, Ann. of Bot., vol. 40, 1926, p. 585.

Fungi.

51. de Bary, Comp. Morph. and Biol. of the Fungi 1887 (1884).

52. Brefeld, Bot. Unters. über Schimmelpilze, Unters aus dem Gesamtgebiet d. Mykologie, vols. 1-15, 1872 to 1912. von Tavel, cf. Morphologie d. Pilze 1892. E. Fischer, Handw. d. Naturw., vol. 7, p. 880. A. Guilliermond, Progr. rei. bot., vol. 4, 1913, p. 389. E. Gäumann, Vergleichende Morphologie der Pilze 1926.

52*a*. Melin, Ber. d. deutsch. bot. Ges., vol. 40, 1922, p. 94, and Svensk. bot. Tidskr., vol. 16, 1922, p. 161. *Id.*, Untersuchungen über die Bedeutung der Baummykorrhiza 1925.

53. Bally, Jahrb. f. wiss. Bot., vol. 50, 1911, p. 95, and Mykol. Zentralbl. II, 1913, p. 289. Gertr. Tobler, Die Synchytrien, Jena 1913. Kusano, Journ. College of Agric., Tokyo 1912, p. 141. G. Schneider (Kartoffelkrebs), Deutsche landw. Presse 1908, Nr. 79, and 1909, Nr. 88. Curtis, Phil. Transact. R. Soc. London, Series B, vol. 210, p. 409. Scherffel, Arch. f. Protistenk., vol. 53, 1925, p. 1. Mattes, *ibid.*, vol. 47, 1924, p. 413.

54. Woronin, Mém. de l'Acad. imp. des Sciences de St. Pétersbourg 1904, 8. Sér., vol. 16, Nr. 4, p. 1. Laibach, Ber. d. deutsch. bot. Ges., vol. 44, 1926, p. 49; Jahrb. f. wiss. Bot., vol. 64, 1927, p. 596.

55. Trow, Annals of bot., vol. 9, 1895, p. 609; vol. 13, 1899, p. 130; vol. 18, 1904, p. 541. Klebs, Jahrb. f. wiss. Bot., vol. 33, 1899, p. 513. Davis, Bot. Gaz., vol. 35, 1903, p. 233. Claussen, Ber. d. deutsch. bot. Ges., vol. 26, 1908, p. 144. Mücke, Ber. d. deutsch. bot. Ges., vol. 26a, 1908, p. 367. von Minden, in Falks Myk. Unt., 3. Heft, 1916, p. 146. Couch, Ann. of Bot., vol. 40, 1926, p. 849.

56. Wager, Annals of bot., vol. 4, 1889–91, p. 127; vol. 10, 1896, pp. 89, 295; vol. 14, 1900, p. 263. Berlese, Jahrb. f. wiss. Bot., vol. 31, 1898, p. 159. Davis, Bot. Gaz., vol. 29, 1900, p. 297. Stevens, Bot. Gaz., vol. 28, 1899, p. 149; vol. 32, 1901, p. 77; vol. 34, 1902, p. 420, and Ber. d. deutsch. bot. Ges. 1901, p. 171. Trow, Annals of bot., vol. 15, 1901, p. 269. Miyake, Annals of bot. 1901, p. 653. Rosenberg, Bihang till Svensk. Ak., vol. 28, 1903. Ruhland, Jahrb. f. wiss. Bot., vol. 39, 1904, p. 135. Rostowzew, Flora 1903, p. 405. Krüger, Zentralbl. f. Bakt., etc., II, vol. 27, 1910, p. 186. Korff and Zattler, Arb. bayer, Landesanst. f. Pflanzenbau, 5. H. 1928.

57. Harper, Annals of bot., vol. 13, 1899, p. 467. Gruber, Ber. d. deutsch. bot. Ges. 1912, p. 126. McCormick, Bot. Gaz., vol. 53, 1912, p. 67. Miss Keene, Annals of bot., vol. 28, 1914, p. 455. Burgeff, Goebels Bot. Abhandl., vol. 4, 1924, p. 1; Flora, vol. 119, 1925, p. 40. Pringsheim and Czurda, Jahrb. f. wiss. Bot., vol. 66, 1927, p. 863.

57*a*. Blakeslee, Bot. Gaz., vol. 42, 1906, p. 161; vol. 43, 1907, p. 415; and vol. 47, 1909, p. 418; Ztschr. f. Bot., vol. 13, 1921, p. 531 (Lit.). Hagem, Vidensk. Selskab. Skrifter, Christiania 1907, No. 7. Burgeff, Ber. d. deutsch. bot. Ges., vol. 30, 1912, p. 679, and Flora, vol. 107, 1914, p. 259; vol. 108, 1915, p. 440. Grete Orban, Beih. Bot. Zentralbl. I, vol. 36, 1919, p. 1. Blakeslee, Bot. Gaz., vol. 72, 1921, p. 179 (Cuninghamella). Burgeff and Seybold, Ztschr. f. Bot., vol. 19, 1927, p. 497.

58. Blakeslee and Gortner, Biochem. Bull. II, 1913, p. 542.

59. Olive, Bot. Gaz., vol. 51, 1906, pp. 192, 229. Lakon, Ztschr. f. ang. Entomol., vol. 5, 1918, p. 161.

60. Raciborski, Flora 1906, p. 106. Fairchild, Jahrb. f. wiss. Bot., vol. 30, 1897, p. 285. Lakon, Jahrb. f. wiss. Bot., vol. 65, 1926, p. 388. Levisohn, *ibid.*, vol. 66, 1927, p. 513.

61. Harper, Jahrb. f. wiss. Bot., vol. 30, 1897, p. 249; further Annals of bot., vol. 13, 1899, p. 467; vol. 14, 1900, p. 321. Guilliermond, Revue génér. de bot., vol. 16, 1904, pp. 49, 130; vol. 33, 1911, p. 89. Claussen, Bot. Ztg. 1905, p. 1. Maire, Compt. rend. soc. bibl., vol. 58, 1905, p. 726. Fraser and Welsford, Annals of bot., vol. 22, 1903, p. 465. Overton (Thecotheus), Bot. Gaz., vol. 42, 1906, p. 450. W. Brown, Bot. Gaz., vol. 52, 1911, p. 275. Schweizer, Ztschr. f. Bot., vol. 15, 1923, p. 529. Schussnig and Becker, Planta, vol. 4, 1927, p. 573.

61*a*. Stoppel, R., Flora, vol. 97, 1907, p. 332. A. Guillermond, Rev. gén. de bot., vol. 21, 1909, p. 401.

62. Blackman and Welsford (Gnomonia), Annals of bot., vol. 26, 1912, p. 761.

Nienburg (Polystigma), Ztschr. f. Bot., vol. 6, 1914, p. 369. Killian (Venturia), Ztschr. f. Bot., vol. 9, 1917. p. 353. Ramlow (Ascoboleae). Mykol. Zentralbl, vol. 5, 1914, p. 177. Dodge, Bull. Torrey bot. Club, vol 41, 1914, p. 157. Killian (Cryptomyces), Ztschr. f. Bot., vol. 10, 1918, p. 49.

63. Schikorra, Ztschr. f. Bot., vol. 1, 1909, p. 379.

64. Falck, Mykol. Unters. u. Ber. II, 1916, p. 77.

65. Harper, Ber. d. deutsch. bot. Ges. 1895, p. 475, and Jahrb. f. wiss. Bot., vol. 29, 1896, p. 655. Neger, Flora 1901, p. 333, and 1902, p. 221. Salmon, Annals of bot., vol. 20, 1906, p. 187. Harper, Carnegie Institution of Washington, publ. No. 37, 1902 (Phyllactinia). Hammarlund, Hereditas, vol. 6, 1925, p. 1.

66. Fraser and Chambers, Annales mycolog., vol. 5, 1907, p. 419.

67. Miehe, Mediz. Klinik 1906, p. 943.

68. Weese, Ber. d. deutsch. bot. Ges., vol. 37, 1919, p. 520.

69. Harper, Annals of bot., vol. 14, 1900, p. 321 (Pyronema). Claussen, Bot. Ztg. 1905, p. 1 (Boudiera), and Ber. d deutsch. bot. Ges. 1906, p. 11. *Id.*, (Pyronema), Ber. d. deutsch. bot. Ges. 1907, p. 586. and Ztschr. f. Bot., vol. 4, 1912, p. 1. Fitzpatrik (Rhizina), Ref. Ztschr. f. Bot., vol. 12, 1920, p. 520.

70. Krombholz, Abb. u. Beschreib. der Schwämme 1831–46. Lenz, Nützl., schdäl. u. verdächt. Schwämme 1890. Further, the works on Fungi, by Gramberg, Michael, Sydow, Schnegg, L. Klein. Dittrich, Ber. d. deutsch. bot. Ges., vol. 34, 1916, pp. 424, 719. A. Ricken, Vademecum für Pilzfreunde 1920, and Die Blätterpilze (Agaricaceae) Deutschlands 1915. Lohwag, H., Verh. zool. bot. Ges. Wien. vol. 35, 1916, p. 38.

70*a*. Dittrich, Ber. d. deutsch. bot. Ges., vol. 35, 1917, p. 27.

71. Fischer, Bot. Ztg. 1908, p. 141. Buchholtz, Ann. mycol., vol. 6, 1908, p. 539. Fischer, Ztschr. f. Bot., vol. 2, 1910, p. 718.

72. Giesenhagen, Flora, Ergzb. 1895, p. 267, and Bot. Ztg. 1901, p. 115. Ikeno, Flora 1901, p. 229, and 1903, p. 1. M. Wieben, Forschungen auf dem Gebiet der Pflanzenkrankh., vol. 3, 1927, p. 139.

73. Guilliermond, Rev. génér. de bot. 1903, p. 49; 1905, p. 337. E. C. Hansen, Zentralbl. f. Bakt., Abt II, vol. 12, 1904. Marchand, Rev. gén. bot. 1913, p. 207. F. Oehlkers, Jahrb. f. wiss. Bot., vol. 63, 1924, p. 142.

74. Thaxter, Mem. of Americ. Acad. Boston 1896, and vol. 13, 1908. Faull, Annals of Bot., vol. 26, 1912, p. 325.

75. R. Lieske, Morph. u. Biol. der Strahlenpilze 1921. Drechsler, Bot. Gaz., vol. 67, 1919, p. 65. Wollenweber, Ber. d. deutsch. bot. Ges. 1921, p. 26.

76. Ruhland, Bot. Ztg. 1901, p. 187. Fries, Ztschr. f. Bot., vol. 3, 1911, p. 145, and vol. 4, 1912, p. 792. Kniep, Ztschr. f. Bot., vol. 3, 1911, p. 531; vol. 5, 1913, pp. 593, 610; vol. 7, 1915, p. 369; vol. 8, 1916, p. 353; vol. 9, 1917, p. 81; Flora, vol. 111, 1918, p. 380; Verhandl. med. phys. Ges. Würzburg, vol. 46, 1920, p. 1; vol. 47, 1922, p. 1; Ztschr. f. ind. Abst.- u. Verarbungslehre, vol. 31, 1923, p. 170; Die Sexualität der niederen Pflanzen, 1928. R. Bauch, Ztschr. f. Bot., vol. 18, 1925, p. 337; Arch. f. Protistenk., vol. 58, 1927, p. 285.

77. Hecke, Ber. d. deutsch. bot. Ges. 1905, p. 248. Lang, Zentralbl. f. Bakt., II, vol. 25, 1910, p. 86, and Ber. d. deutsch. bot. Ges., vol. 35, 1917, p. 4. Rawitscher, Ztschr. f. Bot., vol. 4, 1912, p. 673, and Ber. d. deutsch. bot. Ges., vol. 32, 1914, p. 310, and Ztschr. f. Bot., vol. 14, 1922, p. 273. Werth, Arbeit. Kaiserl. biol. Anst., vol. 8, 1911, p. 427. Paravicini, Ann. mycol., vol. 15, 1917, p. 57. Kniep, Ztschr. f. Bot., vol. 11, 1919, p. 257, and vol. 13, 1921, p. 289; Ztschr. f. Pilzk., N. F., vol. 5, 1926, p. 217. R. Bauch, Biol. Zentralbl., vol. 42, 1922, p. 5; vol. 47, 1927, p. 370; Ztschr. f. Bot., vol. 15, 1923, p. 241; vol. 17, 1925, p. 129. Janchen, Osterr. bot. Ztschr., vol. 72, 1923, p. 302. Sartoris, Amer. Journ. of Bot., vol. 11, 1924, p. 617. Seyfert, Ztschr. f. Bot., vol. 19, 1927, p. 577.

78. Numerous papers by P. Magnus, Klebahn, Sydow, Eriksson, Tischler, E. Fischer, Lagerheim, etc. P. et H. Sydow, Monographia Uredinarum. Maire, Progr. rei bot., vol. 4, 1911, p. 199. Blackman, Annals of bot., vol. 18, 1904, p. 323. Blackman and Fraser, *ibid.*, vol. 20, 1906, p. 35. Christman, Bot. Gaz., vol. 39, 1905, p. 267; Transact. Wisconsin Academy, vol. 15, 1907, p. 517, and Bot. Gaz., vol. 44, 1907, p. 81. Olive, Annals of botany, vol. 22, 1908, p. 331. Dittschlag, Zentralbl. f. Bakt. II, vol. 28, 1910. Kurssanow, Ztschr. f. Bot., vol. 2, 1910, p. 81. Werth and Ludwigs, Ber. d. deutsch. bot. Ges., vol. 30,

1912, p. 523. Fromme, Bot. Gaz., vol. 58, 1914, p. 1. Kurssanow, Ber. d. deutsch. bot. Ges., vol. 32, 1914, p. 317. Lindfors, Svensk. bot. Tidskr., vol. 18, 1924, p. 1. Dodge, Journ. Agric. Res., vol. 31, 1925, p. 641. Zimmermann, Zentralbl. f. Bakt. II, vol. 65, 1925, p. 319. Mordvilko, *ibid.*, vol. 66, 1926, p. 503.

79. Klebahn, Die wirtswechselnden Rostpilze 1904.

80. Eriksson and Tischler, Svenska Vet. Akad. Handl., vols. 37 and 38, 1904. Klebahn, Ber. d. deutsch. bot. Ges. 1904, p. 255. E. Fischer, Bot. Ztg. 1904. p. 327. Marshall Ward, Annals of bot., vol. 19, 1905, p. 1.

81. Hoffmann, Zentralbl. f. Bakt., II, vol. 32, 1911. Werth, *ibid.*, vol. 36, 1912.

81*a*. Kunkel, Amer. journ. of bot., vol. 1, 1914, p. 37.

82. Knoll, Jahrb. f. wiss. Bot., vol. 50, 1912, p. 453, and Ber. d. deutsch. bot. Ges., vol. 30, 1912, p. 36.

83. H. Kniep, Ztschr. f. Bot., vol. 5, 1913, p. 593 ; vol. 7, 1915, p. 365 ; vol. 8, 1916, p. 353. Flora, N. F., vols. 11-12, 1918, p. 380 ; further, Verh. phys. med. Ges. Würzburg, vol. 47, 1922, p. 1. Hirmer, Ztschr. f. Bot., vol. 12, 1920, p. 658.

84. R. Hartig, Der echte Hausschwamm 1885, 2. Aufl., by von Tubeuf 1902. Moller and Falck, Hausschwammforschung., vols. 1-6, 1907–1912. Mez, Der Hausschwamm, Dresden 1908. Falck, Mykolog. Unt. u. Ber. I, 1913.

85. Möller, Pilzgärten südamerik. Ameisen 1893. Holtermann, Schwendener-Festschrift 1899. Forel, Biol. Zentralbl. 1905, p. 170. Huber, Biol. Zentralbl. 1905, p. 606. W. Neuhoff, Bot. Arch., vol. 8, 1924, p. 250.

86. E. Fischer, Denkschr. Schweiz. nat. Ges., vols. 32, 36. Möller, Brasil. Pilzblumen 1895. Atkinson, Bot. Gaz., vol. 51, 1911, p. 1.

Lichenes.

87. Winkler, Pfropfbastarde, I, Teil, 1912, p. 102. Treboux, Ber. d. deutsch. bot. Ges., vol. 30, 1912, p. 77. Nienburg, Ztschr. f. Bot. 1917, p. 530. E. Bachmann, Ztschr. f. Bot., vol. 14, 1922, p. 193 ; Ber. d. deutsch. bot. Ges., vol. 45, 1927, p. 308. F. Tobler, Biologie der Flechten 1925. W. Nienburg, Handb. d. Pflanzenanatomie, vol. 6, 1926. O. Stocker, Flora, vol. 121, 1927, p. 338.

87*a*. K. v. Goebel, Ann. Jard. Bot. Buitenzorg, vol. 36, 1926, p. 1 ; Ber. d. deutsch. bot. Ges., vol. 54, 1926, p. 158.

88. Zopf, Die Flechtenstoffe 1907. Stahl, Häckel-Festschrift 1904, p. 357.

88*a*. Nienburg, Ztschr. f. Bot., vol. 9, 1917, p. 20. Tobler, Ber. d. deutsch. bot. Ges., vol. 37, 1919, p. 364. Linkola, Medd. Soc. fennica, vol. 44, 1918, p. 153.

89. Baur, Flora 1901, p. 319 ; further, Bot. Ztg. 1904, p. 21. Wolff, Flora, Ergzb. 1905, p. 31. Nienburg, Flora, vol. 98, 1908, p. 1. F. Bachmann, Annals of bot., vol. 26, 1912, p. 747.

90. Möller, Kultur flechtenbild. Ascomyceten 1887, and Bot. Ztg. 1888, p. 421. Glück, Flechtenspermogonien, Habilitationsschr. Heidelberg 1899.

90*a*. Freda Bachmann, Arch. f. Zellforschung, vol. 10, 1913, p. 369.

91. Johow, Jahrb. f. wiss. Bot., vol. 15, 1884, p. 361. Möller, Flora 1893, p. 254. Poulsen, Vid. Medd. Kopenhagen 1899.

Bryophyta.

92. Goebel, Organographie II, Bryophyten, 2. Aufl. 1915. Pteridophyten, 2. Aufl. 1918. Campbell, The structure and development of Mosses and Ferns, 2nd edit. 1905. Rabenhorst, Kryptogamenflora, vol. 6. Lebermoose, by K. Müller, vol. 4. Laubmoose, by Limpricht. Loeske, Die Laubmoose, Europas. M. Fleischer, Die Musci der Flora von Buitenzorg, Leyden 1915–1922. F. v. Wettstein, Ztschr. f. ind. Abst. u. Vererbl., vol. 33, 1924, p. 1. Th. Herzog, Geographie der Moose 1926. G. Lorbeer, Ztschr. f. ind. Abst.- u. Vererbl., vol. 44, 1927, p. 1.

93. Goebel, Flora, vol. 90, 1902, p. 279. Davis, Annals of bot., vol. 17, 1903, p. 477. Holferty, Bot. Gaz., vol. 37, 1904, p. 106. Melin, Svensk. Bot. Tidskr., vol. 10, 1916, p. 289. Florin, Arkiv för Bot., vol. 18, 1922, Nr. 5. Showalter, Ann. of Bot., vol. 41, 1927, p. 409.

94. Allen, Archiv f. Zellforschung, vol. 8, 1912, p. 179. Woodburn, Annals of botany, vol. 27, 1913, p. 93. Walker, *ibid.*, p. 116.

95*a*. Zielinski, Flora, vol. 100, 1910, p. 1.

95*b*. Pfeffer, Unters. bot. Inst. Tübingen I, II. Lidfors, Jahrb. f. wiss. Bot., vol. 41, 1904, p. 65. Åkerman, Ztschr. f. Bot., vol. 2, 1910, p. 94.

96. R. Schaede, Beitr. z. Biol. d. Pfl., vol. 14, 1920, p. 27. K. v. Goebel, Flora, vol. 122, 1927, p. 33.

97*a*. Herzfelder, Beih. Bot. Zentralbl. I, vol. 38, 1921, p. 355.

97*b*. Kreh, Nova Acta Acad. Leop., vol. 90, 1909, p. 214. Correns, Unt. über Vermehrung der Laubmoose durch Brutorgane und Stecklinge, Jena 1899. Buch, Brutorgane der Lebermoose, Diss. Helsingfors 1911.

98. Schenck, Bot. Jahrb. f. Syst., vol. 42, 1908, p. 1.

99. Andreas, Flora 1899, p. 161. Douin, Rev. génér. de bot., vol. 24, 1912, p. 392. Clapp (Aneura), Bot. Gaz., vol. 54, 1912, p. 177. K. Meyer (Corsinia), Bull. Soc. imp. des nat. Moskau 1911, p. 263, and Ber. d. deutsch. bot. Ges., vol 32, 1914, p. 262. Schiffner, Progr. rei bot., vol. 5, 1917.

100. Němec, Beih. Bot. Zentralbl., vol. 16, 1904, p. 253. Golenkin, Flora, vol. 90, 1902, p. 209. Schiffner Annales jard. Buitenzorg Supp. III^2, 1910, p. 473. Garjeanne, Flora, vol. 102, 1911, p. 147.

101. Lang, Annals of bot., vol. 21, 1907, p. 201. Campbell, Annals of bot., vol. 21, 1907, p. 467, and vol. 22, 1908, p. 91. Bagchee, Ann. of Bot., vol. 38, 1924, p. 105. G. Lorbeer, Ber. d. deutsch. bot. Ges., vol. 42, 1924, p. 231. D. H. Campbell, Ann. of Bot., vol. 38, 1924, p. 473 ; Flora, vol. 119, 1925, p. 62.

101*a*. Peirce, Bot. Gaz., vol. 42, 1906, p. 55.

102. Goebel, Flora, vol. 101, 1910, p. 43. Gehrmann, Ber. d. deutsch. bot. Ges., vol. 27, 1909, p. 341. Bergdolt, Goebel's bot. Abhandl. 10. H. 1926. Mielnisky, Bot. Arch., vol. 16, 1926, p. 23. O'Hasslon, Bot. Gaz., vol. 82, 1926, p. 215. Förster, Planta, vol. 3, 1927, p. 325.

103. Garber, Bot. Gaz., vol. 37, 1904, p. 161. Lewis, Bot. Gaz., vol. 41, 1906, p. 110 Pietsch, Flora, vol. 103, 1911, p. 347. Black, Ann. of bot., vol. 27, 1913, p. 511. v. Gaisberg, Flora, vol. 114, 1921, p. 362.

104. Haberlandt, Jahrb. f. wiss. Bot., vol. 17, 1886, p. 359. Tansley and Chick, Annals of bot., vol. 15, 1901, p. 1. Correns, Vermehrung der Laubmoose 1899. Vaupel, Flora, 1903, p. 346. Strunk, Diss. Bonn 1914. Grebe, Studien zur Biol. u. Geogr. d. Laubmoose. Hedwigia, vol. 59, 1917. von Dankenschweil, Hedwigia, vol. 57, 1915, p. 14.

105. K. Giesenhagen, Annals jard. Buitenzorg, Suppl. 3^2, 1910, p. 711.

106*a*. Zederbauer, Österr. bot. Ztschr. 1902. Merl, Flora, vol. 109, 1917, p. 189.

106*b* Steinbrinck, Ber. d. deutsch. bot. Ges., vol. 26*a*, 1908, p. 410 ; vol. 27, 1909, p. 169 ; and vol. 28, 1910, pp. 19, 549.

107. Schellenberg, Beih. Bot. Zentralbl. I, vol. 37, 1919–20, p. 115. Fleischer, Ber. d. deutsch. bot. Ges., vol. 38, 1920, p. 84.

108. Haberlandt, Jahrb. f. wiss. Bot., vol. 17, 1880, p. 357. Porsch, Der Spaltöffnungsapparat im Lichte der Phylogenie 1905, p. 33.

109. Bryan, Bot. Gaz., vol. 59, 1915, p. 40. Melin, Svensk. bot. Tidskr., vol. 10, 1916, p. 289.

110. Dihm, Flora, Ergzbd. 1894, p. 286. Goebel, Flora 1895, p. 459. Steinbrinck, Flora, Ergzbd. 1897, p. 131, and Biol. Zentralbl. 1906, p. 727. Kuntzen, Diss. Berlin 1912.

110*a*. Zielinski, Flora, vol. 100, 1909, p. 6.

110*b*. F. v. Wettstein, cf. Nat. Wochenschr. 1922, p. 327.

110*c*. Th. Herzog, Flora, vol. 119, 1925, p. 198.

111. K. von der Dunk, Schistostega. Diss. Frankfurt a. M. 1921.

Pteridophyta.

112. Bower, The origin of a Land Flora, London 1908 ; The Ferns, Cambridge 1923–1926.

113. Pfeffer, Unters. bot. Inst. Tübingen, vol. 1, p. 363 (Ferns, Selaginella). Shibata, Bot. Mag. Tokyo, vol. 19, 1905, p. 39 (Salvinia) ; *ibid.*, pp. 79, 126 (Equisetum) ; Ber. d. deutsch. bot. Ges. 1904, p. 478, and Jahrb. f. wiss. bot., vol. 51, 1905, p. 561 (Isoëtes). Lidfors, Ber. d. deutsch. bot. Ges. 1905, p. 314 (Equisetum). Bruchmann, Flora, vol. 99, 1909, p. 193 (Lycopodium). Buller,

Annals of bot., vol. 14, 1900, p. 543 (Ferns). Shibata, Jahrb. f. wiss. Bot., vol. 49, 1911, p. 1 (Equisetum, Ferns, Salvinia, Isoëtes).

114. Hannig, Flora, vol. 102, 1911, p. 209; vol, 103, 1911, p. 321.

115. Hooker, Synopsis filicum 1883. Baker, Fern Allies 1887. Christ, Farnkräuter der Erde 1897, and Die Geographie der Farne, Jena 1910. Christensen, Index Filicum 1906. A. Th. Czaja, Ber. d. deutsch. bot. Ges., vol. 42, 1924, p. 300. W. Döpp, Pflanzenforschung, 8. H. 1927. D. M. Mottier, Bot. Gaz., vol. 83, 1927, p. 244.

116. Campbell, Annal. Buitenzorg, vol. 22, 1908, p. 99, and Suppl. 3^1, 1910, p. 69. Land, Bot. Gaz., vol. 75, 1923, p. 421.

117. Jeffrey, Univers. of Toronto, biol. series Nr. 1, 1898 (Botrychium). Burlingham, Bot. Gaz., vol. 44, 1907, p. 34 (Ophiogl.). Chrysler, Annals of bot., vol. 24, 1910, p. 1. Lyon, Bot. Gaz., vol. 40, 1905, p. 455 (Botrychium). Bruchmann, Flora, vol. 96, 1906, p. 203 (Botrychium).

118. Steinbrinck, Biol. Zentralbl. 1906, p. 674, and Monatsh. f. d. naturw. Unt., vol. 11, 1918, p. 131.

119. Goebel, Flora, vol. 105, p. 49.

120. Schlumberger, Flora, vol. 102, 1911, p. 383.

121. Arnoldi, Flora, vol. 100, 1909, p. 121. Kundt, Beih. Bot. Zentralbl., vol. 37^1, 1911, p. 26. Zawidski, Beih. Bot. Zentralbl., vol. 28, 1912, p. 17. Yasui, Annals of bot., vol. 25, 1911, p. 469. Lasser, Flora, vol. 117, 1924, p. 173.

121*a*. Pfeiffer, Bot. Gaz., vol. 54, 1907, p. 445. Oes, Ztschr. f. Bot., vol. 5, 1913, p. 145.

122. F. Schneider, Beitr. z. Entw. der Marsiliaceen. Diss. Berlin 1912. Sharp, Bot. Gaz., vol. 58, 1914, p. 419. F. Schneider, Flora, vol. 105, 1913, p. 347. Marshall, Bot. Gaz., vol. 79, 1925, p. 85.

123. Strasburger, Flora, vol. 97, 1907, p. 123.

124. Steinbrinck, Biol. Zentralbl. 1906, p. 724. Hannig, Flora, vol. 102, 1911, p. 209. Ludwigs, Flora, vol. 103, 1911, p. 385. Sharp, Bot. Gaz., vol. 54, 1912, p. 89. Vidal, Ann. sc. nat., 9. Sér., vol. 15, 1912, p. 1.

125. Bruchmann, Flora, vol. 101, 1910, p. 220. Turner, Bot. Gaz., vol. 78, 1924, p. 215. Baranow, Ber. d. deutsch. bot. Ges., vol. 43, 1925, p. 353.

125*a*. Haberlandt, Beitr. z. allg. Bot., vol. 1, p. 293.

126. Bruchmann, Flora, vol. 104, 1912, p. 180; vol. 105, 1913, p. 237; vol. 111, 1919, p. 168, and Ztschr. f. Bot., vol. 11, 1919, p. 39. Lyon, Bot. Gaz., vol. 40, 1905, p. 285. Campbell, Annals of bot., vol. 16, 1902, p. 419. Denke, Beih. Bot. Zentralbl., vol. 12, 1902, p. 182. Steinbrinck, Ber. d. deutsch. bot. Ges. 1902, p. 117, and Biol. Zentralbl. 1906, p. 737. Mitchell, Annals of bot., vol. 24, 1910, p. 19. Sykes and Styles, *ibid.*, p. 523. Wand, Flora, vol. 106, 1914, p. 237. K. v. Goebel, Flora, vol. 122, 1927, p. 393.

127. Steinbrinck, Ber. d. deutsch. bot. Ges., vol. 28, 1910, p. 551, and vol. 29, 1911, p. 334.

128. Bruchmann, Flora 1905, p. 150. Goebel, Flora 1905, p. 195.

129. W. Seyd, Zur Biol. von Selag., Diss. Jena 1910. Neger, Flora, vol. 103, 1911, p. 74.

129*a*. Haberlandt, Ber. d. deutsch. bot. Ges. 1905, p. 441.

130. Lawson and Darnell-Smith, cf. Rev. Ztschr. f. Bot., vol. 12, 1920, p. 89.

130*a*. Kidston and Lang, cf. Ztschr. f. Bot., vol. 12, 1920, p. 583, and vol. 14, 1922, p. 555; Bot. Zentralbl. 1923, p. 121. R. Potonié, Nat. Wochenschr. 1920, p. 822. Gothan, *ibid.*, 1921, p. 399.

131. Stockey, Bot. Gaz., vol. 47, 1909, p. 311. Weber, Hedwigia, vol. 63, 1922, p. 219. Grenda, Bot. Arch., vol. 16, 1926, p. 268.

Fossil Cryptogams.

132. Cf. the Text-books on Palæophytology by W. Ph. Schimper, A. Schenck, B. Renault, G. Saporta et Marion, Solms-Laubach, D. H. Scott, R. Zeiller, A. C. Seward, W. Jongmans. R. Zeiller, Progr. rei bot., vol. 2, 1907, p. 171. Gothan, Potoniés Lehrb. d. Paläobotanik, 2. Aufl. 1920. D. H. Scott, Studies on fossil plants, II, 1923; Genetica, vol. 5, 1923, p. 51. M. Hirmer, Paläobotanik 1927.

133. Gordon, Annals of bot., vol. 24, 1910, p. 821.

134. OLIVER, Biol. Zentralbl. 1905, vol. 25, p. 401, and Annals of bot., vol. 23, 1909, p. 73. SCOTT, Wiss. Ergebn. Wiener bot. Kongr. 1905, p. 279; further, Progr. rei bot., vol. 1, 1907, p. 139, and Smithsonian Report 1907, p. 371. CHODAT, Archives sc. phys. et nat. 4. pér., vol. 26, Genève 1908. OLIVER and SALISBURY, Annals of bot., vol. 25, 1911, p. 1.

135. KIDSTON and LANG, Transact. Roy. Soc. Edinburgh, vols. 51-52, 1917–1922. POSTHUMUS, Rec. trav. bot. néerland., vol. 20, 1923, p. 313. PIA, Ztschr. f. ind. Abst.- u. Vererbl., vol. 35, 1924, p. 29[illegible]. KRÄUSEL and WEYLAND, Senckenbergia, vol. 15, 1923; Abhandl. Senckenberg. naturf. Ges., vol. 40, 1926, p. 114.

SPERMATOPHYTA, BY G. KARSTEN.

Transition from Pteridophyta to Spermatophyta.

1. W. HOFMEISTER, Vergleich. Unters. der Keim., Entfalt. u. Fruchtbildung höherer Kryptogamen und der Samenbildung der Koniferen, Leipzig 1851. E. STRASBURGER, Koniferen u. Gnetaceen, Jena 1872. *Id.*, Angiospermen und Gymnospermen, Jena 1879, and the comprehensive works: R. VON WETTSTEIN, Handb. d. system. Botanik, 3. Aufl., Leipzig and Wien 1924. K. GOEBEL, Organographie der Pflanzen, Jena, 2. Aufl. I. and II. 1913, 1918, and III. 1. 1922, III. 2. 1923, 3. Aufl. I. 1928. J. M. COULTER and CH. J. CHAMBERLAIN, Morphology of Gymnosperms, Chicago 1910. *Id.*, Morphology of Angiosperms, Chicago 1909. The above contain lists of literature, and only fundamental and historically important works or those giving more recent data are referred to here.

2. OVERTON, Reduktion der Chromosomen, Vierteljahrsschr. d. natur. Ges., Zürich 1893. E. STRASBURGER, Reduktionsteilung, Sitzber. K. Akad. d. Wiss., Berlin, vol. 18, 1904. *Id.*, Chromosomenzahlen und Reduktionsteilung. Pringsh. Jahrb., vol. 45, 1908. G. TISCHLER, Allgemeine Pflanzenkaryologie, Berlin 1922.

Morphology and Ecology of the Flower

3. PAYER, Organogénie de la fleur 1857. BAILLON, Histoire des plantes, vols. 1-13, 1867-1894. EICHLER, Blütendiagramme, vols. 1-2, Leipzig 1875 and 1878. A. ENGLER and PRANTL, Natürl. Pflanzenfamilien, vols. 2-4, ab 1889. *Id.*, Das Pflanzenreich, from 1900. BERG and SCHMIDT, Atlas der offizinellen Pflanzen 1863, and 2. Aufl. by A. MEYER and SCHUMANN, 1891–1902, and the literature cited under 1.

4. I am indebted for this to my colleague HEINRICHER. Cf. E. HEINRICHER, Iris pallida Lam., abavia, Biol. Zentralbl. XVI. 13. 1896.

5. CHR. K. SPRENGEL, Das entdeckte Geheimnis der Natur 1793 (OSTWALDS Klassiker, Nr. 48-51). CH. DARWIN, Ges. Werke, Übersetzung von CARUS, vols. 9, 10, 1877. E. WERTH, Über die Bestäubung von Viscum und Loranthus und die Frage der Primitivität der Windblütigkeit wie die Pollenblumen bei den Angiospermen, II. Ber. d. deutsch. bot. Ges. 1923, p. 157. HERM. MÜLLER, The Fertilisation of Flowers by Insects, 1883 (1875), etc. KNUTH, Handbook of Flower Pollination 1906 (1898). O. KIRCHNER, Blumen und Insekten, Leipzig 1911.

6. C. HESS, Exper. Unters. über den angeblichen Farbensinn der Bienen, Zoolog. Jahrb., vol. 34, 1913. *Id.*, Münch. med. Wochenschr. 1914, Nr. 27. *Id.*, Arch. f. d. ges. Physiol., vol. 163, 1916. *Id.*, *ibid.*, vol. 170, 1918. A. KÜHN and R. POHL, Dressurfähigkeit der Bienen auf Spektrallinien. Die Naturwiss., vol. 9, 1921, p. 738.

7. K. VON FRISCH, Der Farbensinn und Formensinn der Biene, Zoolog. Jahrb., vol. 35, 1914. *Id.*, Über den Geruchssinn der Biene, Zoolog. Jahrb., vol. 37, 1919. *Id.*, Zur Streitfrage nach dem Farbensinn der Bienen, Biol. Zentralbl., vol. 39, 3, 1919. *Id.*, Über die Sprache der Bienen, Zoolog. Jahrb., vol. 40, 1923.

8. FR. KNOLL, Insekten und Blumen. Exper. Arb. zur Vertiefung unserer Kenntnisse über die Wechselbeziehungen zwischen Pflanzen u. Tieren, Abh. Zoolog.-Bot. Ges. Wien, vol. 12, 10 Taf., 91 Fig., 1927. *Id.*, Der Tierversuch im Dienste der Blütenökologie, Ber. d. deutsch. bot. Ges. Generalvers. 1922. *Id.*, Über Abendschwärmer und Schwärmerblumen. Ber. d. deutsch. bot. Ges. 1927, p. 510. TH. SCHMUCKER, Beitr. zur Biologie u. Physiologie von Arum maculatum. Flora, vols. 118-119, 1925, p. 460.

9. OTTO PORSCH, Vogelblumenstudien, I. Jahrb. f. w. Bot., vol. 63, 1924.

Id., Biologia generalis, vol. 2, 1926. Bailay, Pollination of Marcgravia, Am. Journ. of bot., vol. 9, 1922, p. 371.

9*a*. G. Tischler, Das Heterostylie-Problem, Biol. Zentralbl., vol. 38, 1918, p. 11. *Id.*, Lythrum Salicaria mit Beziehung auf das Illegimitätsproblem in Festschrift Stahl, Flora 1918. *Id.*, Festschrift Hohenheim 1918, p. 254.

10. K. Goebel, Kleistogame Blüten, Biol. Zentralbl., vol. 24, 1904. H. Ritzerow, Flora 1907. F. Kirchner, Isnardia, Flora in Festschrift Stahl 1918. H. Cammerloher, Kleistopetalie bei Aristolochia arborea, Ber. d. deutsch. bot. Ges., vol. 40, 1923.

Development of the Sexual Generation.

11. Cf. literature under 1, further: Sakugoro Hirasé, Ginkgo biloba, Journ. of the college of science, Univ. imp. Tokio, vol. 8, 1895, and vol. 12, 1898. Jeffrey and Torrey, Ginkgo, Bot. Gaz., vol. 62, 1916. Stefanie Herzfeld, Beitr. zur Kenntnis von Ginkgo, Jahrb. f. wiss. Bot., vol. 66, 1927, p. 814. S. Ikeno, Cycas revoluta, Jahrb. f. wiss. Bot., vol. 27, 1898. H. J. Webber, Spermatogenesis and fecundation of Zamia. U.S. Dep. of agricult., Washington, 1901. Ch. J. Chamberlain, Fertilization and Embryogeny in Dioon edule, Bot. Gaz., vol. 50, 1910. *Id.*, Stangeria paradoxa, Bot. Gaz., vol. 61, 1916, p. 353. P. J. Sedgwick, Life history of Encephalàrtos. Bot. Gaz., vol. 77, 1924. L. G. Reynolds, Female gametophyte of Microcycas, Bot. Gaz., vol. 77, 1924.

12. Cf. literature cited under 1: A. H. Hutchinson, Fertilization in Abies balsamea, Bot. Gaz., vol. 60, p. 457, 5 Taf. 1915. Lancelot Burlinghame, Araucaria brasiliensis, Bot. Gaz., vol. 55, 1913; vol. 57, 1914; vol. 59, 1915. A. Dupler, Taxus canadensis, Bot. Gaz., vol. 64, 1917, p. 115; vol. 68, 1919, p. 345; vol. 69, 1920, p. 492. J. Buchholz, Suspensor and early embryo of Pinus, Bot. Gaz., vol. 66, 1918, p. 185. *Id.*, Polyembryony among Abietineae, *ibidem*, Febr. 1920.

13. W. J. G. Land, Ephedra trifurca, Bot. Gaz., vol. 38, 1907, and *ibidem*, vol. 44, 1907. *Id.*, Veget. Reproduction in an Ephedra, *ibidem*, vol. 55, 1913. J. M. Coulter, Gnetum Gnemon, Bot. Gaz., vol. 46, 1908. O. Porsch, Ephedra campylopoda entomophil, Ber. d. deutsch. bot. Ges., vol. 28, 1910. *Id.*, Nektar von Ephedra, *ibidem*, vol. 34, 1916. O. Lignier et A. Tison, Les Gnétales sont des Angiosperms apétales, Compt. rend. 1911. *Id.*, Les Gnétales, Ann. d. sc. IX. Sér. XVI. M. G. Thoday (Sykes), Gnetum africanum, Ann. of Bot., vol. 25, 1911. Pearson, Microspore of Gnetum, Ann. of Bot., vol. 26, 1912. *Id.*, Welwitschia mirabilis, Phil. Transact. R. soc. 193, 1906, and 200, 1909. Steph. Herzfeld, Ephedra campylopoda, Denkschrift Akad. d. Wiss. Wien, vol. 98, 1922, cf. 19*a*.

14. Literature under 1, further: F. Herrig, Spermazellen im Pollenschlauch der Angiospermen, Ber. d. deutsch. bot. Ges., vol. 37, 1919, p. 456. Rob. B. Wylie, Sperms of Valisneria spiralis, Bot. Gaz., vol. 75, 1923. W. W. Finn, Spermazellen bei Vincetoxicum nigrum und V. officinale, Ber. d. deutsch. bot. Ges., p. 133, 1926. W. Ruhland and K. Wetzel, Der Nachweis von Chloroplasten in den generativen Zellen der Pollenschläuche, Ber. d. deutsch. bot. Ges., vol. 42, 1924.

15. M. Treub, Casuarina, Ann. Buitenzorg, vol. 10, 1891. S. Nawaschin, Lilium Martagon., Bull. acad. imp. St. Pétersbourg 1898. E. Strasburger, Doppelte Befruchtung, Bot. Ztg. II. Abt. 1900. S. Nawaschin, Birke, Mém. acad. imp. St. Pétersbourg. 7. Sér., vol. 42, Nr. 12, 1894. *Id.*, Ulme, Bull. de l'acad. imp. d. sc. de St. Pétersbourg, Sér. V, vol. 8, Nr. 5, 1898. *Id.*, Corylus, *ibidem*, vol. 10, Nr. 4, 1899. *Id.*, Entw. d. Chalazogamen, Mém. acad. usw., 8. Sér., vol. 31, Nr. 9, 1913. M. Benson, Amentiferae, Transact. Linn. Soc. 2. Sér. Bot., vol. 3, pt. 10, 1894. F. A. F. C. Went, Podostemaceen I. and II., Verh. K. Akad v. Wetensch., Amsterdam 1910–12. *Id.*, Development of Podostemaceae, Extr., du recueil des travaux bot. Néerlandais, vol. 5, 1908. W. Magnus, Atypische Embryosackentw. der Podostemaceen, Flora, vol. 105, 1913. O. Dahlgren, Über das Vorkommen von Stärke in den Embryosäcken der Angiospermen, Ber. d. deutsch. bot. Ges. 1927, p. 374. *Id.*, Die Befruchtungserscheinungen der Angiospermen. Hereditas, vol. 10, 1927. P. N. Schürhoff and Frz. J. Jüssen, Nucellarpolyembryonie bei Spathiphyllum Patinii (Hogg) N. E. Br. Ber. d. deutsch. bot. Ges.,

p. 454, 1925. A. E. SHADOWSKY, Über Entwicklung des Embryosackes bei Pancratium maritimum, Ber. d. deutsch. bot. Ges., p. 361, 1925.

15*a*. KARL SCHNARF, Embryologie der Angiospermen (Linsbauer Handb. X-2) 1927–28, K. GOEBEL, In Organographie III, and R. v. WETTSTEIN, Handb., 3. Aufl., gives details as to atypical developments of the embryo-sac and further literature. The same holds for F. L. RUTGERS, The Female gametophyte of Angiosperms. E. J. Brill, Leyden 1923. B. SCHOENEBECK, Die Antipodenvermehrung der Typhaceen, Ber. d. deutsch. bot. Ges., vol. 45, 1924. ARTHUR HAKANSON, Der 16 kernige Embryosack von Azorella bifurcata, Ber. d. deutsch. bot. Ges. 1927, p. 654. ED. QUISUMBING and J. JULIANO, Developm. of ovule and embryosac of Cocos. Bot. Gaz., vol. 84, 1927. A. RADERMACHER, Gametophyten of Nipa, etc., Ann. de Buitenzorg, vol. 35, 1925. ETHEL STIFFLER, Developm. embryosac in Gasteria, Cyrthantus, and Velthemia, Bot. Gaz., vol. 79, 1925.

16. J. HANSTEIN, Entwicklung des Keimes, Bot. Abhandl., vol. 1, 1870. J. GAERTNER, De fructibus et seminibus plantarum, vols. 1, 2, Stuttgart 1789–91. A. P. DE CANDOLLE, Pflanzenphysiologie, German Trans. by ROEPER, vol. 2, p. 212. O. DAHLGREN, Zur Embryologie der Kompositen, insbesondere der Endospermbildung, Ztschr. f. Bot., vol. 12, 1920, p. 481. FR. NETOLITZKY, Angiospermen-Samen, in Linsbauers Handb., vol. 10, 1926.

16*a*. G. BALIČKA-IWANOWSKA, Contrib. à l'étude du sac embryonaire chez certains Gamopetales, Flora 86, 1899.

17. E. STRASBURGER, Chromosomenzahlen, Vererbungsträger, etc., Pringsh. Jahrb., vol. 45, 1908. *Id.*, Apogamie, Parthenogenesis und Reduktionsteilung, Histolog. Beitr., vol. 7, 1909. HANS WINKLER, Parthenogenese u. Apogamie, Progr. rei bot., vol. 2, 1908. C. H. OSTENFELD and O. ROSENBERG, Hieracia, III. O. ROSENBERG, Apogamy in Hieracium, Bot. Tidsskr., vol. 28, 1907. A. ERNST, Bastardierung als Ursache der Apogamie, Jena, G. Fischer, 1918. H. WINKLER, Verbreitung und Ursache der Parthenogenesis im Pflanzen- und Tierreiche, Jena 1920. R. WETTSTEIN, Fakultative Parthenogenesis beim Hopfen, Flora, vols. 118-119, 1925, p. 560.

17*a*. G. HABERLANDT, Experiment. Erzeugung von Aventivembryonen b. Œnothera. Sitzber. Ak. Berlin 40, 1921, and *ibidem* 25, 1921.

17*b*. F. HILDEBRANDT, Verbreitungsmittel der Pflanzen 1873. A. F. W. SCHIMPER, Pflanzengeographie, Jena 1898. W. SCHMIDT, Verbreitung von Samen- und Blütenstaub durch die Luftbewegung. Osterr. Bot. Ztschr., vol. 67, 1918, p. 313. DOCTORS VAN LEEUWEN, Kl. Beitr. zur Kenntnis der endozoischen Verbreitung einiger Hochgebirgspflanzen in Java, Flora, vols. 118-119, 1925, p. 81. RUTGER SERNANDER, Myrmekochoren, Kg. Svensk. Vetensk. Handl., vol. 41, 1906. F. MORTON, Ameisen, etc., Mitt. Naturw. Ver. Univ. Wien 1912.

18. G. KLEBS, Keimung, Unters. bot. Inst. Tübingen, vol. 1, p. 536. J. LUBBOCK, Seedlings, vols. 1, 2, 1892. E. THEUNE, Biologie geokarper Pflanzen. F. COHNS, Beitr., vol. 13, 1916.

Gymnospermae.

19. Literature under 1, 11, 12, and 13 also: K. GOEBEL, Pollenentleerung, Flora, Ergzbd. 1902, p. 237.

19*a*. G. KARSTEN, Gnetum, Cohns Beitr. VI. 1893. P. THOMPSON, Gnetum, Am. Journ. of Bot., 3. 1916.

20. H. D. SCOTT, Palaeozoic botany in Progressus rei bot., vol. 1, Jena 1907, includes the older literature. G. R. WIELAND, American fossil Cycads, 1906, Carnegie Inst. Washington. F. W. OLIVER, Physostoma elegans, Ann. of bot., vol. 23, 1909. *Id.*, and E. J. SALISBURY, Palaeozoic Seeds of the Conostoma group, Ann. of bot., vol. 25, 1911. D. H. SCOTT, The evolution of plants, 1911, London, FERNAND PELOURDE, Les progrès réalisés dans l'étude des Cycadophytes de l'époque secondaire. Progressus rei botanicae, vol. 5, 2. 1916. H. POTONIÉ and W. GOTHAN, Lehrb. d. Paläobotanik, 2. Aufl. 1921. W. GOTHAN, Neuere Arten d. Braunkohlenunters. " Braunkohle " XX. H. 27, 247, 1921, and XXI. H. 22, 1922. R. POTONIÉ, Braunkohle XXI. H. 3-4, 1922. D. H. SCOTT, Notes on palaeozoic Botany, 1907–1927, Recueil des trav. bot. néerl., vol. XXVa, DE VRIES-Festschrift 16. II. 1928. GOLDRING-WINIFRED, 1924, The upper Devonian forest of Seed Ferns in Eastern New York, N. Y. Mosner Bull. 251. KRÄUSEL and WEYLAND,

1926, Beitr. zur Kenntnis der Devonflora, III. Abt., Senckenberg. Naturf. Ges., vol. 40, Frankfurt. W. H. Lang, 1925, the Contr. to Study of the Old Red Sandstone flora of Scotland: Trans. of the Royal Soc. of Edinburgh, vol. LIV, 1926, I-V.

Angiospermae Dikotylae.

21. E. A. Newell Arber, Origin of Angiosperms, Journ. Linn. Soc., vol. 38, 1907, p. 263. Mez and Gohlke, Physiologisch-systematische Untersuchungen über die Verwandtschaften der Angiospermen, Cohns Beitr., vol. 12, 1913. Mez and Lange, Ranales, *ibidem*, vol. 12, 1913. Mez and Preuss, Parietales, *ibidem*, vol. 12, 1914. Mez and Kirstein, Gymnospermen, *ibidem*, vol. 14, 1920. Also numerous papers in Bot. Arch., vols. 1-10, 1920–25. Further works on Serodiagnotic are collected in the lists of publications by Fedde. H. Ziegenspeck, Bot. Arch., 17, 1927.

22. R. v. Wettstein, Sammelref. Die Bedeutung der sero-diagnostischen Methode für die phylogenetisch-systematische Forschung. Ztschr. f. Indukt.-Abst.-lehre, vol. 36, Heft 3-4, 1925. E. Stolley, Die Psilophyten, Geolog. Verein Hannover 1925. *Id.*, Zur Kritik der Königsberger Serodiagnostik, *ibidem*, 1925. *Id.*, Das Ende der Königsberger Serodiagnostik, *ibidem*, 1927. E. Gilg and P. N. Schürhoff, Erfahrungen über die Brauchbarkeit der Serodiagnostik für die botanische Verwandtschaftsforschung, Ber. d. deutsch. bot. Ges., vol. 45, 1927. J. Boerner and B. Helwig, Beitr. zur serolog. Systematik der Pflanzen, Bibliotheca botanica, vol. 94, 1927. Walter Nay, Serodiagnost. Verwandtschaftsforschungen innerhalb der Rosales, Myrtiflorae u. Umbelliflorae, Cohns Beitr., vol. 15, 2. 1927. H. G. Zarnack, Beitr. über die Brauchbarkeit der Serodiagnostik für die botan. Verwandtschaftsforschungen, Ranales, *ibidem*, 1927. Hannig and Slatmann, Phytoserolog. Untersuch. I., Planta, vol. 5, 1. 1928.

23. Literature 1 and 3, further: S. Murbeck, Verhalten des Pollenschlauches von Alchemilla arvensis und das Wesen der Chalazogamie, Lunds Univ. Arsskr., vol. 36, 1901, p. 6. H. Hallier, Verwandtschaftsverhältnisse bei Englers Rosalen, Parietalen, Myrtifloren usw., Abhandl. d. Naturw. Vereins Hamburg 1903, contains notes on previous publications by the same author. Karl Schnarf, Embryologie der Angiospermen (Linsbauers Handb. d. Pflanzenanatomie), vol. 10, 2, 1927–28. Edmund W. Sinnot, Investigations on the phylogeny of the Angiosperms I-III, Americ. Journ. of Bot., vol. 1, 1914. Walther P. Thompson, The morphology and affinities of Gnetum, Americ. Journ. of Bot., vol. 3, 1916. Arber and Parkin, On the Origin of Angiosperms, Journ. Linn. Soc. London. Bot. vol. 38, p. 29, 1907. J. Hutchinson, The families of flowering plants, I. Dicotyledons, London 1926. L. Diels, Käferblumen bei den Ranales und ihre Bedeutung für die Phylogenie der Angiospermen, Ber. d. deutsch. bot. Ges., vol. 34, 1916. E. Strasburger, Drimys Flora, Ergzbd. 1905. G. Karsten, Zur Phylogenie der Angiospermen, Ztschr. f. Bot., vol. 10, 1916, p. 369.

23*a*. E. Sargant, Origin of monocotyledons, Ann. of bot., vol. 17, 1903, and Bot. Gaz., vol. 37, 1904. K. Fritsch, Stellung der Monokotyledonen, Beibl. 79 to Englers Bot. Jahrb., vol. 34, 1905. J. Nitzschke, Beitr. z. Phylogenie d. Monokotyledonen 1914. Cohns Beitr., vol. 12. O. Liehr, Ist die angenommene Verwandtschaft der Helobiae und der Polycarpicae auch in ihrer Zytologie zu erkennen? Cohns Beitr., vol. 13, 1916.

24. Hans Winkler, Rafflesia aus Zentralborneo, Planta, vol. 6, 1927.

25. H. Hallier, Hammalidaceae, Beih. Bot. Centralbl., vol. 14, 1913.

26. Marloth, Kapland, Valdivia-Exped., vol. 23, 1908. *Id.*, Mimicry among Plants, Transact. S. Afr. Philos. Soc., vols. 15, 16, 1904–5. *Id.*, Schutzmittel der Pflanzen gegen übermäßige Insolation, Ber. d. deutsch. bot. Ges., vol. 26, 1909.

27. Raph. Bauer, Entwicklungsgesch. Untersuch. an Polygonaceenblüten, Flora, vol. 115, 1922. F. Roth, Die Fortpflanzungsverhältnisse bei der Gattung Rumex Diss. Bonn 1907.

28. Cf. p. 462 and literature 15*a*.

29. E. Heinricher, Immunität der Birnenbäume gegen die Mistel, Ber. d. deutsch. bot. Ges., vol 48, 1926. *Id.*, Über d. Anschluß d. Loranthoideae a. d. Wirte usw., Bot. Arch., vol. 15, 1926. *Id.*, Ist für die Anlage der Haustorien der Santalaceen chemische Reizung oder Kontakt wirksam ? Ak. Wien 1926.

30. H. Graf zu Solms-Laubach, Herkunft usw. des gew. Feigenbaumes, Abh. d. K. Ges. d. Wiss., Göttingen 1882. Fritz Müller, Caprificus u. Feigenbaum, Kosmos, vol. 6, 1882. A. Tschirch, Die Feigenbäume Italiens, Ficus Carica *a* Caprificus und Ficus Carica *β* domestica und ihre Beziehungen zueinander, Ber. d. deutsch. bot. Ges., vol. 29, 1911. M. Treub, L'organ femelle et l'embryologie dans le Ficus hirta, Ann. Buitenzorg, vol. 18, 1902.

31. K. Goebel, Schleuderfrüchte bei Urticifloren, Flora, vol. 108, 1915. *Id.*, Entfaltungsbewegungen 333, Jena 1920. A. R. Bechtel, Floral anatomy of the Urticales, Am. Journ. of bot., vol. 8, 1921, p. 386. M. Treub, L'apogamie de l'Elatostemma acuminatum, Ann. Buitenzorg, vol. 20, 1906.

32. O. Warburg, Kautschukpflanzen, Berlin 1900. E. Ule, Kautschukpflanzen der Amazonasexped Englers Jahrb., vol. 35, 1905.

32*a*. R. Wettstein, Fakultative Parthenogenesis beim Hopfen, Flora 1925.

33. Büsgen, Fagales in Kirchner, Loew, Schroeter, Lebensgesch. d. Blütenpfl., vol. 2, 1. 1913. W. Troll, Über die weibl. Partialinfloreszenzen von Pasania Mig. u. Quercus L., Ber. d. deutsch. bot. Ges. 1926, p. 290. The works of Nawaschin and Benson cited in 15.

34. Hildur Ljungdahl, Zur Zytologie der Gattung Papaver, Svensk. Bot. Tidskr., vol. 16, 1922. E. Heinricher, Schlauchzellen der Fumariaceen, Ber. d. deutsch. bot. Ges., vol. 5, 1887.

35. H. Graf zu Solms-Laubach, Cruciferenstudien, vols. 1-4, Bot. Ztg., 1900–1906. E. Heinricher, Über Eiweißstoffe führende Idioblasten bei einigen Cruciferen, Ber. d. deutsch. bot. Ges., vol. 2, 1884.

35*a*. G. Klebs, Nachkommen künstlich veränderter Blüten von Sempervivum. Ak. Heidelberg 1909.

36. Gunnar Täkholm, On the Cytology of the Genus Rosa, Svensk. Bot. Tidskr., vol. 14, 1920, p. 300. K. Goebel, Bot. Ztg. 1882, p. 353. A. de Candolle, Ursprung der Kulturpflanzen 1884. H. Graf zu Solms-Laubach, Erdbeeren, Bot. Ztg., vol. 1, 1907, p. 45. F. Noll, Pfropfbastarde von Bronveaux, Sitzber. Niederrhein. Ges. Bonn 1906.

37. Th. Belt, Naturalist in Nicaragua 1888, p. 218. Alfred Möller, Pilzgärten der südamerikanischen Ameisen. (Bot. Mitteilungen aus den Tropen von A. F. Schimper, vol. 6, 1893.) Lothar Geissler, Zur Morphologie der Infloreszenzen und Blüte von Neptunia oleracea, Ber. d. deutsch. bot. Ges., vol. 36, 1927.

38. L. Diels, Südwest-Australien, Veg. d. Erde, vol. 7, 1906.

38*a*. A. F. W. Schimper, Indo-Malayische Strandflora, Jena 1891. G. Karsten, Mangrovevegetation, Bibliotheca botanica, vol. 22, 1891.

39. H. de Vries, Mutationstheorie 1901–1903. The extensive literature on Œnothera is collected in Fr. Oehlkers Erblichkeitsforschung an Pflanzen, Wiss. Forschungsber., vol. 18, 1927.

40. J. Schweiger, Euphorbiaceen, Flora, vol. 94, 1905. A. Markowski, Gattung Pedilanthus, Diss. Halle 1912. Heinr. Schmidt, Entwicklung der Blüten u. Blütenstände von Euphorbia usw., Beih. Bot. Zentralbl., vol. 22, 1907.

40*a*. O. Stocker, Über transversale Kompaßpflanzen. Flora 1926.

41. A. de Candolle, Ursprung der Kulturpflanzen 1884. V. Hehn, Kulturpflanzen u. Haustiere, 7. Aufl. 1902. On bizarre forms, cf. E. Strasburger, Pfropfhybriden, Pringsh. Jahrb., vol. 54, 1907, p. 538.

41*a*. P. Baranov, Zur Morphologie u. Embryologie der Weinrebe, Ber. d. deutsch. bot. Ges., vol. 97, 1927.

42. F. Tobler, Die Gattung Hedera 1912. *Id.*, Die Gartenformen der Gattung Hedera, Deutsch. dendrol. Ges. 1927.

42*a*. W. Troll, Über d. Staubblattkrümmungen der Umbelliferen, Flora 1916. H. St. Jurica, Morph. study of the Umbelliferae, Bot. Gaz., vol. 76, 1922, p. 292. A. Hakansson, Entwicklungsgesch. der Umbelliferen. Lunds Univ. Arsskr., N. F., Avd. 2. 18. 1923.

43. A. Nestler, Cortusa Matthioli, Ber. d. deutsch. bot. Ges. 1912, p. 330. Ossian Dahlgren, Selbsterilität von Lysimachia nummularia, Hereditas III, 1922.

44. P. Graebner, Heide, Veget. d. Erde, vol. 5, 1901. A. Artopoeus, Ericaceen, Flora 1903. Gunnar Samuelson, Entwicklungsgesch. d. Blüten einiger Biscornestypen, Svensk. Bot. Tidskr. 1913.

45. O. Dahlgren, Embryologie der Loganiaceen-Gattung Spigelia, Svensk. Bot. Tidskr., vol. 16, 1922, p. 77.

46. R. von Wettstein, Österr. bot. Ztschr. 1900. *Id.*, Denkschr. k. k. Akad. d. Wiss. Wien, vol. 69, 1896.

47. E. Gilg, Strophanthus, Tropenpfl. 1902. *Id.*, H. Thoms, H. Schedel, Ber. d. deutsch. pharmaz. Ges. 1904.

48. Cf. under **32**; also P. Preuss, Exp. nach Zentral- u. Südamerika, Berlin 1901. Warburg, Kunene-Sambesi-Exped., Berlin 1903.

49. M. Treub, Ann. de Buitenzorg, vol. 3, 1883.

50. Hans Winkler, Unters. über Pfropfbastarde, vol. 1, Jena 1912. *Id.*, Über experimentelle Erzeugung von Pflanzen mit abweichenden Chromosomenzahlen, Ztschr. f. Bot., vol. 8, 1916, p. 417.

50*a*. G. Klebs, Über erbliche Blütenanomalien beim Tabak. Zeitschr. f. induktive Abst. u. Vererb., vol. 17, 1916.

51. E. Heinricher, Lathraea, Ber. d. deutsch. bot. Ges. 1893. *Id.*, Grüne Halbschmarotzer 1-4, Jahrb. f. wiss. Bot. 1897, 1898, 1901, 1902, 1909, 1910. R. von Wettstein, Monogr. Euphrasia 1896. Sterneck, Alectorolophus 1901.

52. K. Goebel, Morph. u. biol. Studien 5, Ann. de Buitenzorg, vol. 9. *Id.*, Flora, vol. 98, 1904. E. Merl, Utricularien, Flora, vol. 108, 1915. A. Th. Czaja, Fangvorrichtung der Utriculariablase, Ztschr. f. Botanik, vol. 14, 1922, p. 705.

53. M. Treub, Myrmecodia, Ann. de Buitenzorg, vol. 3, 1883, p. 129. H. Miehe, Javanische Studien, Abh. Kgl. Sächs. Akad. d. Wiss., vol. 32, Nr. IV, Leipzig 1911.

53*a*. F. C. von Faber, Das erbliche Zusammenleben von Bakterien u. trop. Pflanzen, Jahrb. f. wiss. Bot., vol. 51, p. 285, Leipzig 1912. *Id.*, Die Bakteriensymbiose der Rubiaceen, *ibidem*, vol. 54, 1924, p. 243. Fr. E. Lloyd, Rubiaceen, 1 and 2, Torrey bot. Club, vol. 8, 1902.

54. F. Noll, Cucurbitaceen, Landw. Jahrb., 30. Ergzbd. P. 1901. *Id.*, Parthenokarpie, Sitzber. Niederrh. Ges. Bonn 1902. Cf. also **63**. G. Bitter, Bryonia, Abh. Nat. Ver. Bremen 1904. C. Correns, Bestimmung u. Vererbung des Geschlechts, Berlin 1907. J. Kratzer, Verwandtschaftliche Beziehungen der Cucurbitaceen, Flora, vol. 110, 1918, p. 275.

55. L. Jost, Griffelhaare der Campanulaceen, Flora, Festschrift Stahl, vol. 111, 1918.

56. R. E. and Th. C. E. Fries, Die Riesenlobelien Afrikas, Svensk. Bot. Tidskr., vol. 16, 1928, p. 383.

57. Rob. E. Fries, Zur Kenntnis der Compositen des trop. Ostafrika, Acta Horti Bergiensi, vol. 9, 1928. R. E. and Th. C. E. Fries, Die Riesensenecionen der afrikanischen Hochgebirge, Svensk. Bot. Tidskr., vol. 16, 1922, p. 321. P. N. Schürhoff, Synergidenhaustorien bei Calenduleae u. Arctotideae, sowie d. systematische Stellung der Compositen, Ber. d. deutsch. bot. Ges. 1926, p. 665. K. Miyake, Wachstum des Blütenschaftes von Taraxacum Beih. Bot. Zentralbl., vol. 16, 3. 1904. O. Rosenberg, Unters. über d. Chromosomenverh. in Crepis, Svensk. Bot. Tidskr., vol. 14, 1920, p. 319. Cf. Ostenfeld and Rosenberg under **17**.

Monocotylae.

58. Literature 23*a* and O. Porsch, Abstammung der Monokotylen und die Blütennektarien, Ber. d. deutsch. bot. Ges., vol. 31, 1913, p. 580.

58*a*. J. C. Schoute, Verdickungsweise des Stammes von Pandanus. Ann. d. Buitenzorg, 2. Sér., VI. 1907. *Id.*, Pneumatophoren v. Pandanus, *ibidem*, 2. Sér., Suppl. III. 1909.

59. E. Strasburger, Verdickungsweise von Palmen, Jahrb. f. wiss. Bot., vol. 34, 1906. Gr. Kraus, Ann. de Buitenzorg, vol. 24, 1911. J. C. Schoute, Dickenwachst. der Palmen, Ann. de Buitenzorg, vol. 26, Leiden 1912.

60. Peter Stark, Variabilität des Laubblattquirls bei Paris quadrifolia, Ztschr. f. Bot., vol. 1, 1915. *Id.*, Blütenvariationen der Einbeere, Ztschr. f. Abstammungs- u. Vererbungslehre, vol. 19, 1918.

60*a*. H. Schlimbach, Beitr. zur Kenntnis der Samenanlage und der Samen der Amaryllidaceen mit Berücksichtigung des Wassergehaltes der Samen, Flora, vol. 117, 1924, p. 41.

61. K. Goebel, Streptochaeta, Flora 1895, Ergzbd. J. Schuster, Grasblüte, Flora, vol. 100, 1910. F. Koernicke, Handb. d. Getreidebaues, vol. 1, Bonn 1885. Alph de Candolle, Kulturpflanzen, Leipzig 1884. G. Schneider, Vegetationsvers. mit 88 Hafersorten (in two kinds the ligule is wanting), Landwirtsch. Jahrb., vol. 42, 1913, p. 767 ff. Aug. Schulz, Geschichte des Weizens, Ztschr. f. Naturw. 1911. *Id.*, Geschichte des Spelzweizens, Abh. Naturf. Ges. Halle 1917–18.

62. E. Hannig, Pilzfreies Lolium, Bot. Ztg. 1907.

63. G. Tischler, Parthenokarpe Angiospermer Früchte, Jahrb. f. wiss. Bot., vol. 52, 1912. Josef Schachner, Beitr. zur Kenntnis der Blüten- und Samenentwicklung der Scitaminaceen, Flora, vol. 117, 1924, p. 1. A. d'Angermond, Parthenokarpie bei Bananen, Ber. d. deutsch. bot. Ges., vol. 30, 1913. W. Herrmann, Blattbewegung der Marantaceen, Flora, vol. 109, 1916, Diss. Jena. J. C. Costerus, Bau der Blumen von Canna und derjenigen der Marantaceen, Ann. de Buitenzorg, 2. Sér., vol. 15, 1916.

64. H. Burgeff, Zur Biologie der Orchideen-Mykorrhiza, Diss. Jena 1909.

65. H. Fitting, Beeinflussung der Orchideenblüte durch die Bestäubung usw., Ztschr. f. Bot., vol. 1, 1909. *Id.*, Entwicklungsphysiolog. Unters. an Orchideenblüten, Ztschr. f. Bot., vol. 2, 1910. M. Hirmer, Organographie der Orchideenblüte, Flora, N. F., vol. 13, 1919, p. 213. O. von Kirchner, Über Selbstbestäubung bei den Orchideen, Flora, 1922, p. 103. Süssenguth, Über Pseudogamie bei Zygopetalum Mackeyi Hook., Ber. d. deutsch. bot. Ges. 1923, p. 16.

CORRECTION

Cetraria islandica (pp. *474, *477, 478) is no longer official in Great Britain
delete OFFICIAL on pp. 477 (Fig. 445) and 478.

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